

PERICALINE LEBIINI: NOTES ON CLASSIFICATION, A SYNOPSIS
OF THE NEW WORLD GENERA, AND A REVISION OF THE
GENUS *PHLOEOXENA* CHAUDOIR (COLEOPTERA: CARABIDAE)

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The subtribe *Pericalina* is a diverse, moderately divergent tropicopolitan subtribe of lebiine Carabidae, defined by possession of one or more pairs of setae ventrally on the head capsule, elongate labrum, falcate female styli bearing large spines, and asetose ventral grooves of the mandibles. The *Pericalina* include *Mormolyce* Hagenbach, as well as most other genera variously treated as pericalines, coptoderines, catascopines, and thyreopterines.

The 11 New World genera are distinguished in a key, and their characteristics are described and illustrated. Four groups of genera are recognized: "thyreopteroids" — *Phloeoxena* Chaudoir, *Oreodicastes* Mairon, *Stenognathus* Chaudoir, *Ochropisus* Bates, and *Catascopus* Kirby; "somotrichoids" — *Somotrichus* Seidlitz and *Catascopellus* Straneo; "eurycoleoids" — *Stenoglossa* Chaudoir, *Lelis* Chaudoir and *Eurycoleus* Chaudoir; "pericaloids" — *Coptodera* Dejean. The genus *Stenognathus* includes three subgenera: *Pristolomus* Chaudoir, *Phloeotherates* Bates, and *Stenognathus* sensu stricto. *Ferus* (= *Stenognathus*) *quadrifolius* Chaudoir, 1869, a junior secondary homonym of *S. quadrifolius* Chaudoir, 1843, is renamed *Stenognathus* *chaudoiri*. Described and illustrated is the new species *Ochropisus* *concolor* (type locality — MEXICO, Morelos, 9.1 mi. E. Cuernavaca, 4300'). A key is provided to the species of *Ochropisus* and to the Mexican species of *Catascopus*.

The genus *Phloeoxena* Chaudoir includes 16 species, arrayed in three subgenera. *Tacana*, new subgenus, includes only *P. herculeano*, new species, (type locality — MEXICO, Chiapas, Volcan Tacaná, SE slope, 7800', cloud forest). The 11 species of subgenus *Phloeoxena* are in the *schwarzi* and *picta* groups, with the seven species of the *schwarzi* group known only from the West Indian Greater Antilles, and the four species of the *picta* group occurring in Middle America. The following new taxa of the nominotypical subgenus are described and illustrated: *P. megalops* *erwinorum* (type locality COSTA RICA, Puente Arenas, 1.5 km. NE Monteverde, along antenna road, 10°19'N, 84°44'W, 1500-1700 m); *P. nigricollis* (type locality MEXICO, Chiapas, San Quentin, 16°24'N, 81°20'W, 700'), *P. picta* *batesi* (type locality GUATEMALA, San Geronimo); *P. picta* *franiae* (type locality GUATEMALA, Dpto. Huehuetenango, Cuchumatanes Mts., 5.6 mi. N. Santa Cruz Barillas, 1280 m); *P. picta* *apicalis* (type locality MEXICO, Oaxaca, 16.9 mi. S. Valle Nacional, 3600'). *Phloeoxena* *graphiptera* var. *limbicollis* Bates is given species status, and *Phloeoxena* *unicolor* Chaudoir is treated as a subspecies of *P. picta*. The names *P. picta* Chaudoir and *P. graphiptera* Chaudoir are synonymized, with the former name the senior synonym.

A reconstructed phylogeny of *Phloeoxena* is presented in conjunction with historical zoogeography based on geological history of the circum-Caribbean area, and the known geographical and ecological ranges of the species. It is proposed that the ancestor of *Phloeoxena* arose in South America, dispersed northward in early-mid-Tertiary time, to nuclear Central America, and there differentiated, with various stocks later dispersing to and differentiating in the West Indies, in Mexico north of the Isthmus of Tehuantepec, and in lower central America.

Les Pericalina, une sous-tribu des lebiini dans la famille des Carabidae, est un groupe diverse, modérément différencié, et cosmopolite dans les tropiques. Nous définissons cette sous-tribu

par la possession d'une ou plusieurs paires de soies ventrales sur la capsule cephalique, un labre allongé, de larges éperons sur les styles falciformes de la femelle, par l'absence de soies dans les sillons ventraux des mandibules. Les *Pericalina* incluent les *Mormolyce* Hagenbach, de même que divers autres genres traités comme des péricalines, des coptodérines, des catascopines et des thyréopterines.

Nous séparons à l'aide d'une clef les onze genres du nouveau monde, et nous décrivons et illustrons leurs caractéristiques. Nous reconnaissons quatre groupes de genres: les "thyréopteroides" — *Phloeoxena* Chaudoir, *Oreodicastes* Maindron, *Stenognathus* Chaudoir, *Ochropisus* Bates, et *Catascopus* Kirby; les "somotrichoides" — *Somotrichus* Seidlitz et *Catascopellus* Straneo; les "eurycoloides" — *Stenoglossa* Chaudoir, *Lelis* Chaudoir, et *Eurycoleus* Chaudoir; les "péricaloides" — *Coptodera* Dejean. Le genre *Stenognathus* inclue trois sous-genres: *Pristolomus* Chaudoir, *Phloeotherates* Bates, et *Stenognathus* sensu stricto. *Ferus* (= *Stenognathus*) *quadricollis* Chaudoir, 1869, un homonyme secondaire récent de *S. quadricollis* Chaudoir, 1843, est renommé *Stenognathus chaudiroides*. Nous décrivons et illustrons la nouvelle espèce *Ochropisus concolor* (localité-typique — MEXICO, Morelos, 9.1 mi. E. Cuernavaca, 4300'). Nous pourvoyons une clef des espèces d'*Ochropisus* et des espèces mexicaines de *Catascopus*.

Le genre *Phloeoxena* Chaudoir inclue seize espèces, distribuées dans trois sous-genres. *Tacana*, un nouveau sous-genre, inclue seulement une nouvelle espèce *P. herculeano*, (localité typique — MEXICO, Chiapas, Volcan Tacana, pente du SE, 7800', forêt des nuages). Nous séparons les espèces du sous-genre *Phloeoxena* en deux groupes: *schwarzi* et *picta*. Les sept espèces du groupe *schwarzi* ne se trouvent que dans les Grandes Antilles, et les quatre espèces du groupe *picta* ne se rencontrent qu'en Amérique moyenne (Amérique centrale et le Mexique). Nous décrivons et illustrons les nouvelles espèces suivantes du sous-genre *Phloeoxena*: *P. megalops erwinorum* (localité typique — COSTA RICA, Puente Arenas, 1.5 km. NE Monteverde, le long de la route de l'antenne, 10°19'N, 84°44'W, 1500-1700 m); *P. nigricollis* (localité typique — MEXICO, Chiapas, San Quentin, 16°24'N, 81°20'W, 700'); *P. picta batesi* (localité typique — GUATEMALA, San Geronimo); *P. picta franiae* (localité typique — GUATEMALA, Depart. Huehuetenango, montagnes du Cuchumatanes, 5.6 mi. N. Santa Cruz Barillas, 1280 m); *P. picta apicalis* (localité typique — MEXICO, Oaxaca, 16.9 mi. S. Valle Nacional, 3600'). *Phloeoxena graphiptera* var. *limbicollis* est considéré comme espèce, et *Phloeoxena unicolor* Chaudoir devient une sous-espèce de *P. picta*. Les noms *P. picta* et *P. graphiptera* deviennent synonymes, avec le premier nom comme synonyme ancien.

Nous présentons une phylogénie reconstruite en relation avec une histoire zoogéographique basée sur l'histoire géologique de la région des Antilles, et sur nos connaissances de la distribution géographique et de l'habitat de chaque espèce. Nous proposons que l'ancêtre des *Phloeoxena* a évolué en Amérique du sud d'où il s'est dispersé vers le nord, au début des temps tertiaire moyen, jusqu'au noyau de l'Amérique centrale. Là ils se différencièrent et produisirent d'autres souches qui se dispersèrent et se différencièrent dans les Antilles, au Mexique au nord de l'isthme de Tehuantepec, et au sud de l'Amérique centrale.

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INTRODUCTION

The montane cloud forests of Middle America¹, small in extent and now dwindling rapidly because of the ravages of land-starved hominid primates, are repositories for remnant lineages of organisms that arose in teeming forests of the Neotropical lowlands and lower mountain slopes, and have since been replaced there by later-evolving forms. Understanding of the phylogenetic patterns of extant taxa is often made possible by discovery of relict groups, so the geographical areas where they are likely to occur have a special fascination for evolutionary biologists. Added to this, the feeling of solitude and inner peace that these misty, verdant havens engender make them a naturalists' paradise. So it was that Donald R. Whitehead and I sought them out during our travels in Mexico in 1965-66.

A clear morning in February, 1966 found us collecting in a small patch of cloud forest on the northern slopes of a high mountain near Motozintlá, Chiapas. The carabid fauna proved to be magnificently diverse, and the bromeliads yielded an especially rich harvest of specimens varying in shape, size and color. Of this impressive lot, three specimens stood out: they were not especially large, and they were dull in color (piceous). At first, we took them to be agonines of the subgenus *Rhadine*, even though no members of this group are known to be arboreal, nor to live so far south in Mexico. Then, noting the truncate elytral apices and pectinate tarsal claws, we considered that they might be lebiines, but if so, to what genus did they belong? In the end, we left our question unanswered, to be pursued at some later date.

That date occurred about a year ago, after I had failed to find comparable material on three trips to museums housing major collections of Middle American Carabidae. In the meantime, I had decided that these specimens represented a group of lebiines. Further examination showed that they were near *Phloeoxena*, and this led to the question of defining this genus. From this point, it was but a series of short steps to general questions involving lebiine classification, and especially classification of the group to which *Phloeoxena* belongs, called by Habu (1967) the subtribe Pericalina.

This paper provides a general though superficial consideration of pericaline classification, a more detailed consideration of the New World pericaline genera, and still more detailed treatment of the species of *Phloeoxena*. To this last-named genus belong the three specimens that we collected some nine years ago.

MATERIALS AND METHODS

Material. — This paper is based on study of approximately 500 specimens of pericaline lebiines, about 50 per cent of which represent the genus *Phloeoxena*, 35 per cent represent other New World pericaline genera, and 15 per cent represent Old World taxa. This last-named group includes: *Thyreopterus* Dejean (five species); *Pericalus* MacLeay (six species); *Nycteis* Castelnau (three species); *Lobodontus* Chaudoir (two species); *Labocephalus* Chaudoir (two species); *Eurydera* Castelnau (four species); and *Catascopus* Kirby (10 species). Additionally, one or two specimens of each of the following genera were checked, to confirm that their external characteristics were those of the Pericalina: *Sinurus* Chaudoir; *Peripristus* Chaudoir; *Stenotelus* Chaudoir; *Holcoderus* Chaudoir; *Minuthodes* Chaudoir; *Agonochila* Chaudoir; *Philophloeus* Chaudoir; *Moctherus* Schmidt-Goebel; and *Miscelus* Klug.

Sources of material are the collections of the following institutions, indicated in the text by these abbreviations:

1. Mexico and Central America.

AMNH	Department of Entomology, American Museum of Natural History, New York;
BMNH	Department of Entomology, British Museum (Natural History), London, England;
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts;
MNHP	Entomologie, Museum National d'Histoire Naturelle, Paris, France;
UAIC	Department of Entomology, University of Arkansas, Fayetteville, Arkansas;
UASM	Strickland Museum, Department of Entomology, University of Alberta, Edmonton, Alberta, Canada;
USNM	Department of Entomology, United States National Museum of Natural History, Smithsonian Institution, Washington, D. C.

Borrowed type material was returned to the lending institutions. Holotypes and allotypes of new taxa from material in the Strickland Museum were deposited in the USNM. Paratypes were distributed to major institutions with important holdings of Neotropical Carabidae.

Methods. — Taxonomic principles, criteria for recognition of species-group taxa and the general working methods have been explained in previous publications (Ball, 1970 and 1972; Ball and Nègre, 1972), and are not repeated here.

Measurements were used to indicate variation in size and proportions. The following measurements were made, using an ocular micrometer in a Wild M5 Stereoscopic Binocular Microscope, at a magnification of 25X:

- length of labrum — measured along edge, from base to apex;
- width of labrum — maximum transverse distance;
- length of mentum — greatest length of mental lobe, from base to apex;
- width of mentum — maximum transverse distance;
- length of head — linear distance from base of left mandible to posterior margin of left compound eye;
- width of head — maximum distance dorsally across head, including compound eyes;
- length of pronotum — linear distance from anterior to posterior margin, measured along the mid-line;
- width of pronotum at apex — maximum transverse distance between anterior angles;
- pronotum, maximum width — greatest linear transverse distance;
- width of pronotum at base — maximum transverse distance between posterior angles;
- length of elytra — linear distance from basal ridge to apex of longer elytron, measured along the suture.

These measurements were added or combined in ratios, as follows:

SBL — standardized body length: sum of length of head, pronotum and elytra;

L: l/w — labrum: length/width;

M: 1/w — mentum: length/width;

Hw/Pwm — width of head/maximum width of pronotum;

Hw/Pl — width of head/length of pronotum;

P: Aw/Bw — Pronotum: width of apex/width of base;

Pl/El — length of pronotum/length of elytra.

Dissections were made using standard techniques. Genitalia and other small structures were preserved in glycerine in plastic or glass microvials, pinned beneath the specimens from which the parts were removed.

Microsculpture was studied and photographed using a Cambridge Mark IV "Stereoscan" Scanning Electron Microscope.

THE SUBTRIBE PERICALINA

Diagnostic characteristics. — Based on characteristics of adults, the subtribe *Pericalina* is here defined as follows: Lebiini; ventral surface of head behind submentum with one or more pairs of “suborbital” setigerous punctures, each seta about as long as supraorbital setae; labrum elongate, at least 0.57 as long as wide, longer than clypeus, more or less tapered toward apical margin (Fig. 64); mandibles without setae in ventral grooves (Fig. 65 C, D); members of most genera without terebral teeth; labium of most groups with paraglossae longer than ligula, latter with two or more setae apically (Fig. 2, 6, 8, 10, 13); middle coxae each with three or more setae on lateral margin; tarsus without brush-like dense hairs on ventral side, article 4 simple, not emarginate or bilobed at apex; each elytron of most members with penultimate puncture of umbilical series displaced laterally, against marginal groove (Fig. 43 A); ovipositor falcate, acuminate toward apex, with one spine on inner margin on dorsal side, and two or three spines on outer margin at ventral side (Fig. 4 C, 11, 33); habitat tree trunks and fallen logs on forest floor.

The character states of the labium and ovipositor are plesiotypic; the others are apotypic.

This diagnosis includes the Pericali of Lindroth (1968: 1014); Somotrichini (Lebiinae) of Mateu (1963); Coptoderitae of Hansen (1968); Cymindina in part, Pericalina, and Catascopina of Habu (1967: 77-117); the Catascopi of Jedlička (1963: 295-297); the Coptoderitae, Thyreopteritae and Pericalitae of Basilewsky (1953: 205-211); the Singilini in part (Lebiinae-Lebiidae), Coptoderitae (Lebiidae), and Thyreopteridae of Jeannel (1949: 922-946, 1006-1039); the Pericalinae of Bates (1883 and 1869); the Coptoderides and Thyreopterides of Chaudoir (1869 a and b); and the Pericalides of Lacordaire (1854: 137-149), with a few additions and deletions. Except for *Somotrichus* and *Mormolyce*, the group as here recognized is coincident with the Catascopi of Csiki (1932: 1352-1385), the explicit opinions of Jeannel and Basilewsky notwithstanding. (The latter author (1953: 210) included the Thysanotini in the Thyreopterinae, but I doubt that this is a correct allocation). These authors used characters of doubtful significance for grouping genera. These characters were: presence or absence of serrulations of the tarsal claws (varies between genera whose members are otherwise markedly similar to one another); basal margin of pronotum beaded (thickened) or not (this feature is individually various within genera). In marked contrast to these authors, Habu recognized only two subtribes for this complex of genera, isolating in its own subtribe the genus *Catascopus*. However, this genus and the other pericalines share the apotypic character states listed above, and are otherwise distinguishable from one another only by tarsal form (“slender” in Pericalina; “stout” in Catascopina). He also included *Somotrichus* in the Cymindina, but the members of this genus exhibit the apotypic character states of the Pericalina.

The long “suborbital” setae are characteristic of adults of the New Zealand lebiine *Actenonyx bembidioides* White. However, the character states of labrum, mandibles, labium, umbilical series and ovipositor are unlike those of the Pericalina. Hence, the genus *Actenonyx* is not a pericaline. (For further information about the genus *Actenonyx*, see Britton, 1941.)

Desirable as it would be to propose a detailed classification for the Pericalina, I am unable to do so at present. The subtribe is probably old as suggested by its Gondwanian distribution, with more or less extensive endemism on each continent of the Southern Hemisphere. Probably the best procedure in working out relationships is to compare *inter se* the genera of each continent, and then to make inter-continental comparisons. The system outlined below is based mainly on consideration of New World taxa.

The position of Mormolyce. — This remarkably distinctive Oriental genus, members of which Jeannel described as possibly the most baroque of any insect species, has been variously located among the Carabidae. Originally thought to be a pterostichine, it was placed in the Thyreopterides

by Chaudoir (1869a: 133); in a monobasic tribe by Horn (1881: 149), (based on, among other features, a unique organization of the pterothoracic sclerites), near the Odacanthini and Ctenodactylini; in a subfamily of its own by Bates (1869: 72), and Rousseau (1906: 1), but they so ranked all of the tribes of Horn; in a subfamily of its own by Csiki (1928: 3), who recognized only two other subfamilies of Carabidae, Carabinae and Harpalinae. Jeannel (1949: 1010) returned it to the company of the thyreopterines and placed it with several Madagascan genera having large, broad deplanate members, in the Mormolycini, subfamily Thyreopterinae. This arrangement was accepted by Basilewsky (1953: 210).

Although *Mormolyce* is clearly "pericaloid" in the broadest sense, I doubt that it is close to any other extant genus. The mandibles (Fig. 1 A and B) are so plesiotypic that I believe the genus belongs at the base of the pericaline stem, as a putative representative of a very early lineage. I also think that the Madagascan genera whose members are large and broadly explanate evolved this form independently of *Mormolyce*. Mandibles, (Fig. 5 and 7) and labia (Fig. 6 and 8) of two such genera, *Labocephalus* and *Eurydera*, are illustrated for comparative purposes. (See also illustrations of the labium (Fig. 2) and ovipositor sclerites (Fig. 4) of female *Mormolyce*, as further evidence of pericaloid affinities.)

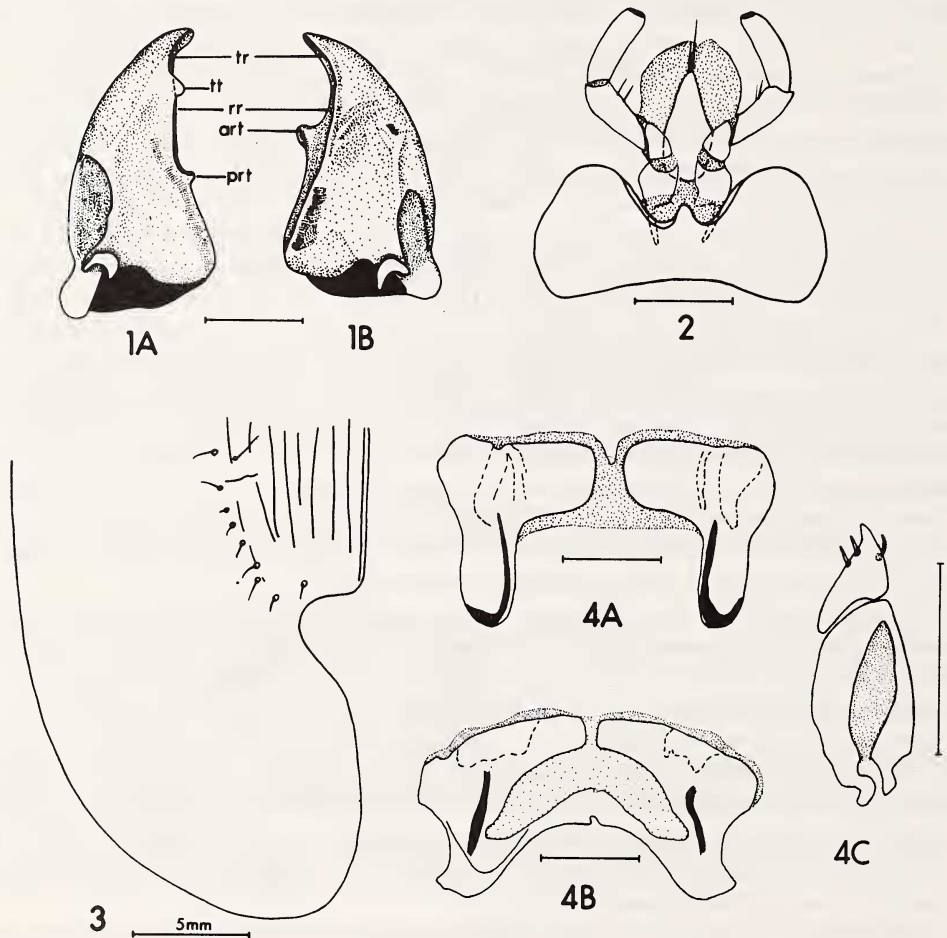


Fig. 1-4. *Mormolyce phyllodes* Hagenbach. — Fig. 1. Mandibles, dorsal aspect; A, left; B, right. — Fig. 2. Labium, ventral aspect. — Fig. 3. Left elytron, apical portion. — Fig. 4. Ovipositor and associated sclerites: A, tergum VIII, dorsal aspect; B, sternum VIII, ventral aspect; C, coxite and stylus, ventral aspect.

Highly apotypic character states of adults in addition to the markedly flattened, explanate body with broad lateral flanges of the elytra are: elongate head with four pairs of ventral head setae; elongate flattened appendages; mesepimeron and metepisternum attaining the middle coxal cavities; recurved tarsal claws; and the absence of secondary sexual differences (Lieftinck and Wiebes, 1968: 60). An additional structural feature, not previously noted, is the form of the apex of antennal article 11, and its large preapical sensory setae (Fig. 14 A, B). Fig. 15 represents the type of article 11 characteristic of all other pericalines and most other carabids. Another apotypic feature is the reduced upper spur of the front tibia. The larva seems to be highly distinctive both in structure (with only a single claw per tarsus and mandibles each with a very large retinacular tooth (Van Emden, 1942: 20)), and in habitat (chambers in large shelf fungi (Lieftinck and Wiebes, 1968: 66-67)).

Even though this genus possesses the apotypic character states of the Pericalina, should it be included in this group? In view of its autapotypic features, is it desirable to place *Mormolyce* in a group of its own, independent of pericalines, of tribal or even higher rank? Because this genus is probably the sister group of all other pericalines, cladists would rank it equal to all the others together. Phenetic-Phyletic classifiers (self-styled "evolutionary" school), would also follow this course because of the marked evolutionary divergence of *Mormolyce*. However, I place this genus in the subtribe Pericalina to emphasize its relationships. I think such emphasis is much more important than drawing attention to its strikingly unique character states.

THE NEW WORLD PERICALINA

Characteristics shared by all or most New World pericalines are recorded here, and are not repeated in the generic descriptions.

Microsculpture. Meshes transverse on ventral surface of head, and thoracic and abdominal sterna.

Head. Two pairs of supraorbital setigerous punctures. Frontal impressions various, in most groups shallow, indistinct, broad; vertex with shallow transverse impression behind eyes. Compound eyes large, bulged. Antennae of moderate length, extended slightly beyond elytral humeri; articles 2 and 3 with ring of setae at apices, 3 with few setae preapically; article 4 setose in apical half; articles 5-11, setose throughout length. Clypeus transverse, anterior margin truncate or slightly concave.

Mouthparts. Labrum various, narrow, in most groups slightly wider than long. Mandibles generally elongate, trigonal at base, falcate anteriorly, with well developed scrobes baso-laterally; ventrally, ventral grooves and pre-molar-molar areas without setae. Left mandible (Fig. 65 A, C): terebral ridge short, tooth absent; cutting edge retinacular ridge, latter long; anterior retinacular tooth absent, posterior retinacular tooth small; premolar tooth small, premolar ridge short. Right mandible (Fig. 65 B, D): terebral ridge longer than on left mandible, terebral tooth absent; anterior retinacular tooth and posterior retinacular ridge well developed, posterior terebral tooth absent; premolar tooth small, but larger than on left mandible; molar and premolar areas thin, not thickened.

Maxillae elongate, otherwise average for Lebiini (Fig. 66); stipes with one long baso-lateral seta in most groups (two in *Catascopus*).

Labium: ligula more or less narrow; paraglossae as long or longer than ligula and adnate to it basally; palpiger asetose (except *Coptodera*); penultimate article of labial palpus with two setae on anterior margin, both near apex in members of most groups.

Prothorax. Pronotum various in shape, dorsal surface deplanate or disc slightly convex; median longitudinal impression shallow, anterior and posterior lateral impressions more or less clearly indicated, posterior-lateral impressions basin-like, continuous anteriorly with broad

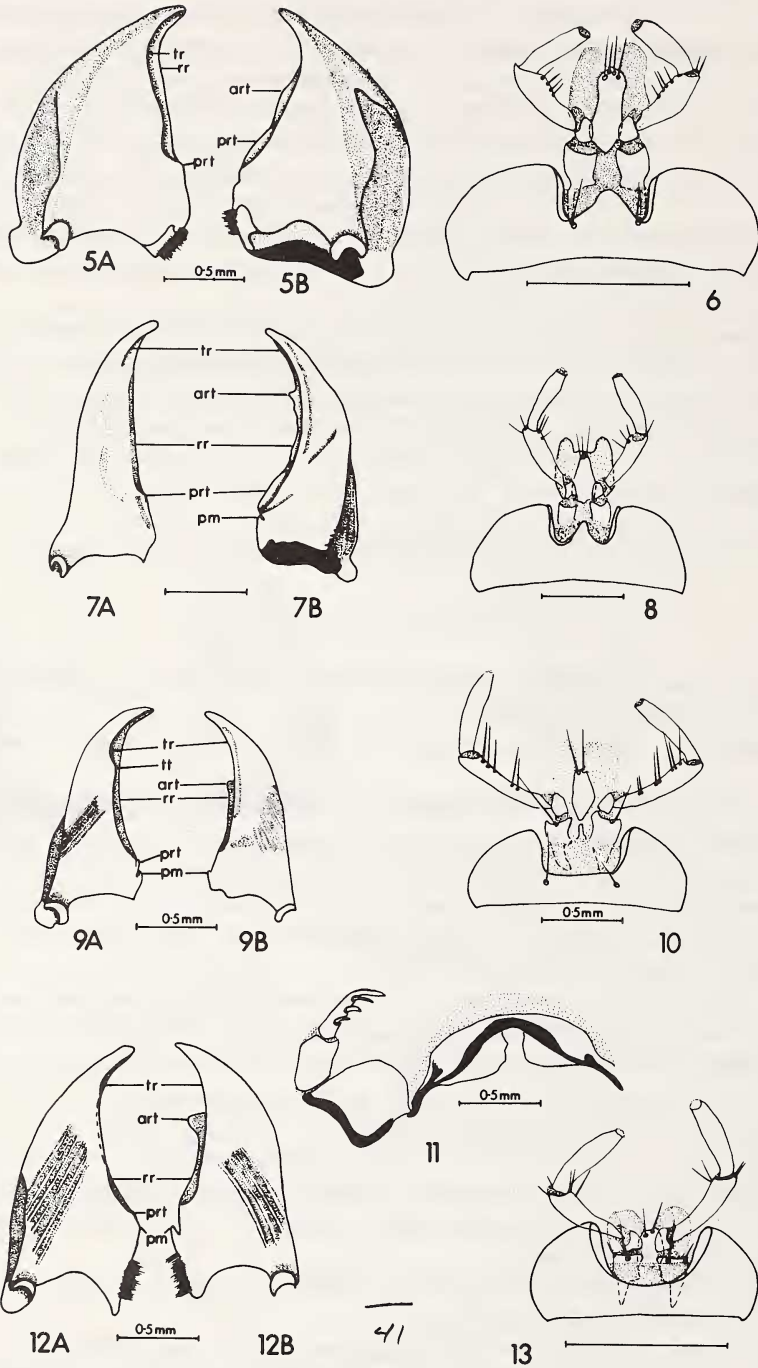


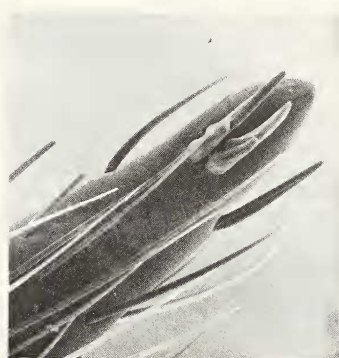
Fig. 5-6. *Labocephalus longipennis* Castelnau, female. Fig. 5. Mandibles, dorsal aspect; A, left; B, right. Fig. 6. Labium, ventral aspect. Fig. 7-8. *Eurydera lugubrina* Fairmaire, female. Fig. 7. Mandibles, dorsal aspect: A, left; B, right. Fig. 8. Labium, ventral aspect. Fig. 9. *Pericalus guttatus* Chevrolat, female. Mandibles, dorsal aspect: A, left; B, right. Fig. 10-11. *Pericalus ornatus* Schmidt-Goebel, female. Fig. 10. Labium, ventral aspect. Fig. 11. Ovipositor, coxite and stylus. Fig. 12-13. *Nycteis brevicollis* Castelnau. Fig. 12. Mandibles, dorsal aspect: A, left; B, right. Fig. 13. Labium, ventral aspect.

ANTENNAL ARTICLES OF *Mormolyce phyllodes* and *Labocephalus striatus*



14A

50μ



14B

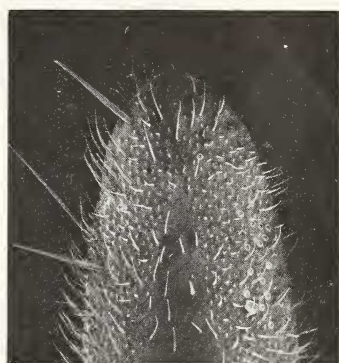
50μ



15A

100μ

20μ



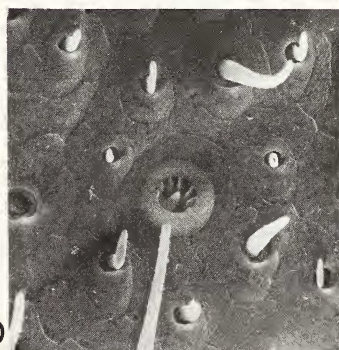
15B

50μ

5μ



15C



15D

Fig. 14-15. Stereoscan photographs of articles 10 and 11 of antenna. Fig. 14. *Mormolyce phyllodes* Hagenbach, female: A, article 11 terminal portion, lateral aspect; B, terminal portion, ventral aspect. Fig. 15. *Labocephalus striatus*, female: A, articles 10 and 11, lateral aspect; B, article 11, terminal portion, lateral aspect; C, article 11, lateral aspect, contrasting central glabrous area and lateral setose areas; D, article 11, lateral aspect, showing coeloconic sense organ.

lateral grooves; two pairs of lateral setae (except *Oreodicastes* and *Phloeoxena montana* Darlington). Prosternum with apex of intercoxal process not beaded.

Pterothorax. Metepisternum in most groups longer than wide, metasternum medially longer than middle coxal cavity.

Elytra. Various in shape and proportions, each elytron with shallow lateral depression slightly posterior to humerus, latter in most groups broadly rounded. Scutellar stria evident (except *Oreodicastes*). Discal punctures three (in subgenus *Tacana*, usually more); umbilical series more or less broadly interrupted medially, of 13-16 setigerous punctures in most groups (more in subgenus *Tacana*); penultimate puncture displaced laterally more or less, either in or close to marginal groove. (Fig. 43 A).

Legs. Average for Lebiini; tibiae with thin spines; tarsal articles dorsally each with pair of setae near apex; tarsal claws pectinate (in most groups) or not.

Abdomen. Sterna III - VI with pair of ambulatory setae; sternum VII with one or two pairs near apical margin, latter shallowly notched in males, entire in females.

Male genitalia. Median lobe compressed, basal part small.

Female ovipositor. Tergum VIII pair of lateral apodemes, membranous medially (Fig. 69 A); sternum VIII as in Fig. 69 B; tergum X as in Fig. 69 C; valvifer as in Fig. 69 D; stylus more or less falcate, with apical part subequal in length to basal part, and with single spine along inner margin, two or three spines along outer margin (Fig. 69 E).

Note about mandibles. — Modifications of the general arrangement described above affect the form, but not the cutting edges. For example, the mandibles are deplanate in members of *Lelis* (Fig. 53) and *Eurycoleus* (Fig. 56), and the scrobes are shallow and indistinct, more markedly so in the latter genus.

I have not studied in detail the mandibles of other lebiine groups; most of them seem to have setae in the ventral grooves and differ from pericalines in structure of their cutting edges.

Notes on classification. — Because of a shortage of multiple-character correlations, uncertainties about the pattern of phylogeny and personal lack of detailed knowledge of the Old World pericaline fauna, I can present here only a few tentative observations.

It is desirable to state the relationships of the New World genera to the Old World pericalines.

One genus, the widespread *Somotrichus* (including the single species *S. unifasciatus* Dejean) is almost certainly introduced from the Old World. Its members share with those of *Catascopelus* a setulose dorsal surface, dentate mentum, short paraglossae and lobate base of the pronotum. Two genera, *Coptodera* and *Catascopus*, have counterparts in the Old World tropics that I regard as respective congeners. I share this view with Habu (1967: 78), and thereby differ from the views expressed by Jeannel (1949: 924) and Basilewsky (1953: 208). The remaining genera seem to be without congeneric relatives in the Old World Tropics. They key either to, or in the vicinity of, the "Coptoderitae", but they are not closely related to *Coptodera*. The genera *Phloeoxena*, *Oreodicastes*, *Stenognathus* and *Ochropisus* seem to be close to *Catascopus*, sharing with the last-named genus similar mouthparts and not differing in any consistent combination of distinctive features. However, in body form the members of the New World endemic genera (except *Oreodicastes*) tend to be rather flattened, whereas the members of *Catascopus* are more slender and robust. In turn, the character states of *Catascopus* are not far removed from those of the Old World thyreopterine genera, as the latter group was defined by Jeannel.

Like members of *Coptodera*, those of *Stenoglossa*, *Lelis* and *Eurycoleus* lack a mental tooth. However, unlike members of *Coptodera*, members of these genera lack also a seta from each palpiger. I doubt that these endemic New World groups are closely related to *Coptodera*.

I believe that a smooth (non setulose) dorsal surface, toothed mentum, paraglossae longer than ligula, glabrous palpigera and smooth tarsal claws are plesiotypic (shared with agonines

and other more plesiotypci carabids), and judge taxa having these features to be themselves plesiotypic. Apotypic groups, then, are the ones with setulose dorsal surfaces, edentate menta, short paraglossae, setigerous palpi, and pectinate tarsal claws.

Although the features characterizing the New World genera near *Catascopus* are plesiotypic, and although it is best not to base taxa on symplesiotypic character states, I am tentatively grouping them as the "thyreopteroid" genera with their Old World dentate counterparts. The "somotrichoid" stock, characterized above, includes the genera *Somotrichus* and *Catascopellus*. This complex is obviously close to the thyreopteroids, and perhaps it should be included therein. This complex is discussed more fully under the genus *Somotrichus*. The edentate *Coptodera* is the sole New World representative of the "pericaloid" stock, characterized additionally by the setigerous palpi. (For comparative purposes, illustrations are provided of mouthparts and ovipositor of *Pericalus*, and mouthparts of *Nycteis*, both Old World pericaloid genera. See Fig. 9-13. See also Hansen (1968) for an account of the African members of this complex.) Finally, the genera characterized by a combination of edentate mentum, asetose palpi and short paraglossae are placed in a group of their own, the "eurycoleoid" genera.

Further study is needed of the edentate, non-pericaloid genera to answer two important questions: 1) are the New World and Old World genera closely related, or was each edentate geographical group derived independently from the dentate thyreopteroid stock; 2) what are the relationships of the pericaloids to these other edentate groups? It is important to answer these questions, as Noonan (1973) and Reichardt (1974) answered similar ones about harpalines and helluonines, respectively.

In summary, the New World genera and subgenera are arranged as follows:

"Thyreopteroids"

- Phloeoxena* Chaudoir
- Oenaphelox*, new subgenus
- Tacana*, new subgenus
- Phloeoxena* (*sensu stricto*)
- Oreodicastes* Maindron
- Stenognathus* Chaudoir
- Stenognathus* (*sensu stricto*)
- Pristolomus* Chaudoir
- Phloeotherates* Bates
- Ochropisus* Bates
- Catascopus* Kirby
- Catascopus* (*sensu stricto*)

"Somotrichoids"

- Somotrichus* Seidlitz
- Catascopellus* Straneo

"Eurycoleoids"

- Stenoglossa* Chaudoir
- Lelis* Chaudoir
- Eurycoleus* Chaudoir

"Pericaloids"

- Coptodera* Dejean
- Coptodera* (*sensu stricto*)

Notes on evolutionary trends. — This is a preliminary attempt to interpret some of the divergence in structure and habits noted within this subtribe. Pericalines presumably represent or are near to the basal stock of the Lebiini, and developed from "platynoid" (Pterostichini)

ancestors. Such ancestors probably were moderately flat, with dark, concolorous integument, and smooth tarsal claws — that is, similar to extant members of the genus *Platynus*. They were probably arboreal, like many extant agonines.

With reference to body form of adults, two major trends are evident. First, is the tendency for the body to become flattened and explanate. Probably this is associated with life beneath fairly tight-fitting bark, or in crevices on logs. Second, is the tendency to evolve a form reminding of tiger beetles, and called here "cicindeloid". The first trend reaches its apogee in *Mormolyce*, but various lines of thyreopteroids exhibit it, as does the eurycoleoid stock. The cicindeloid trend is seen in *Pericalus* among the pericaloids, and in *Catascopus* among the thyreopteroids. Adults of many of these species are diurnal and evidently do their hunting on tree trunks (Darlington, 1968: 102), as do various stocks of arboreal tiger beetles.

Other structural trends seem to involve development of pectinate tarsi, loss of the mental tooth and reduction of the mental lobes. Each of these has probably occurred several times. Transverse microsculpture has probably evolved many times from the plesiotypic isodiametric pattern, and the scaled type has developed several times in various groups of *Phloeoxena* (see Fig. 114, and discussion of elytral microsculpture under "Evolutionary considerations"). The median lobe of the male genitalia underwent torsion several times so that the apical orifice is ventral in position rather than dorsal. (I follow Jeannel (1949) in terming the plesiotypic condition (without torsion) "anopic", and the apotypic condition (with torsion) "catopic").

Color and pattern are generally associated with mode of life: bright metallic colors characterize diurnal cicindeloid pericalines (as well as some of the nocturnal ones); somber colors, such as black, shades of brown and of dull yellow characterize groups whose adults lead a more concealed existence. Generally, the pattern of a bi-colored dorsum is such as to suggest disruptive concealing coloration, but at least some members of *Eurycoleus* mimic beetles of the family Erotylidae (Erwin, pers. comm.), and the blue and red color pattern of members of *Lelis* suggest mimicry of similarly colored adults of *Lebia*. So, evolution of color seems to be three-directional: 1) development of bright metallic color; 2) retention of dark color, but development of a disruptive pattern (see Fig. 16, 44 and 47); and 3) development of mimicry. Possibly, these trends have been reversed in various lines, with a reversion to the concolorous condition (see Fig. 115).

Little is known about food habits. The mouthparts suggest carnivory, and Erwin (pers. comm.) demonstrated that *Eurycoleus* preys on fungivorous endomychids. Larvae and adults of *Mormolyce* seem to have an even more intimate association with fungi, but the relationship has not been studied in detail: do they eat the fungus, or do they feed on fungivorous insects? Members of *Stenognathus* are also associated with fungi (Bates, 1869: 80). Habu (1967: 75) notes that individuals of *Somotrichus unifasciatus* Dejean prey on adults and larvae of *Tribolium castaneum* Herbst. Probably the ancestors of the Pericalina were generalized carnivores, and various lines acquired more specialized feeding habits.

Although the flattened body form is adaptive for life beneath bark of trees, it is also adaptive for life in other types of confined spaces. Thus, it is not surprising that some pericalines live on the ground, among leaf litter in forests (Darlington, 1968: 112). In the New World, some pericalines residing in cloud forests are found on the ground, as are individuals of some species of *Coptodera*, at lower elevations.

The somotrichoids seem to have diverged significantly from other pericalines in way of life, and have entered a new adaptive zone. For instance, members of *Somotrichus unifasciatus* Dejean survive long voyages in stored products, and as a result the species has become widespread (Habu, 1967: 75. Darlington, 1968: 83). Members of the species *Oecornis nidicola* Britton, 1940 are known only from the nests of hornbills of the species *Bycanistes cristatus* Rüppel, and members of *Paulianites nidicola* Jeannel, 1949 inhabit the nests of weaver-birds

of the species *Foudia sakalava*. Other somotrichoids are found in more prosaic places, such as the vicinity of swamps in decaying vegetation — atypical for pericalines, as a whole.

The African somotrichoids have converged in size, color and body vestiture with the African lichnasthenines and singilines (Mateu, 1963).

Key to New World Genera and Subgenera of Subtribe Pericalina

- 1 Mentum with median tooth 2
- 1' Mentum without median tooth (Fig. 60) 13
- 2 (1) Dorsal surface of body setulose; pronotum with posterior margin lobate 3
- 2' Dorsal surface glabrous (with few long tactile setae, only); pronotum with posterior margin truncate 4
- 3 (2) Color dark, elytra concolorous; eyes reduced, head with prominent temporal lobes; tarsal claws smooth *Catascopellus* Straneo, p. 171
- 3' Color pale, elytra bicolored (Fig. 43 E); eyes bulged, large, head without prominent temporal lobes; tarsal claws pectinate *Somotrichus* Seidlitz, p. 169
- 4 (2') Hind tibia with dorsal (outer) surface longitudinally canaliculate (one groove extended length of tibia) 5
- 4' Hind tibia with dorsal surface rounded, smooth or longitudinally strigulose (numerous short irregularly spaced grooves and ridges), or keeled, but not canaliculate 6
- 5 (4) Tarsal claws smooth, not pectinate; dorsum metallic green *Catascopus* Kirby, p. 166
- 5' Tarsal claws pectinate, dorsum uniformly piceous or bicolored, not metallic *Ochropisus* Bates, p. 163
- 6 (4') Elytron with microsculpture meshes approximately isodiametric, or longitudinal and parallel to long axis of body; surface dull (most specimens), or shining (few specimens) *Phloeoxena* Chaudoir 8
- 6' Elytron with microsculpture meshes transverse, surface shining 7
- 7 (6') Pronotum with hind angles broadly rounded (Fig. 20), without lateral setae *Oreodicastes* Maindron, p. 156
- 7' Pronotum with hind angles obtuse or rectangular, not broadly rounded (Fig. 21-23), with two pairs lateral setae *Stenognathus* Chaudoir 11
- 8 (6) Elytron with humerus diagonally sloped (Fig. 18), umbilical punctures about 20, in more or less continuous row; discal punctures 3 to 9 *Tacana*, new subgenus, p. 182
- 8' Elytron with humerus broadly rounded, (Fig. 16, 17, 19), umbilical series 9 to 15 punctures, with more or less wide diastema medially; discal punctures 2 or 3 9
- 9 (8') Specimen from locality in West Indies . . . subgenus *Phloeoxena* (in part), p. 156
- 9' Specimen from mainland locality 10
- 10 (9') Elytra with microsculpture meshes broad, adjacent ones in contact at margins, without linearly arranged narrow, high keels (Fig. 102, 104) *Oenaphelox*, new subgenus, p. 205
- 10' Elytron with microsculpture meshes narrow, high keels, linearly arranged (Fig. 85) subgenus *Phloeoxena* (in part), p. 184
- 11 (7') Tarsal claws pectinate; dorsal surface of hind tibia smooth subgenus *Phloeotherates* Bates, p. 162
- 11' Tarsal claws smooth, not pectinate; dorsal surface of hind tibia longitudinally strigulose 12
- 12(11') Elytron with lateral margin smooth, preapical angle rounded, not toothed (Fig. 21) subgenus *Stenognathus* (*sensu stricto*), p. 161

- 12' Elytron with lateral margin serrate, preapical angle toothed (Fig. 22) subgenus *Pristolomus* Chaudoir, p. 162
- 13 (1') Mentum with lateral lobes pointed or narrowly rounded apically (Fig. 49 B and 60, M: 1/w ca. 0.40 or more); mandibles slender, not explanate basally 14
- 13' Mentum with lateral lobes subtruncate apically (Fig. 54 and 57, M: 1/w ca. 0.35 or less); mandibles moderately to strongly explanate basally (Fig. 53 and 56) ... 15
- 14(13) Pronotum approximately truncate basally, not lobed (Fig. 47); hind tibia with dorsal surface keeled; palpiger of labium with seta ventrally (Fig. 60); sternum VII of abdomen narrowly notched apically *Coptodera* Dejean, p. 176
- 14' Pronotum with base lobed medially; hind tibia with dorsal surface rounded, not keeled; palpiger of labium glabrous; sternum VII of abdomen notched *Stenoglossa* Chaudoir, p. 172
- 15(13') Body very broad; pronotum and elytra broadly explanate; mandibles broadly explanate; ligula with four or five setae; paraglossae setose laterally *Eurycoleus* Chaudoir, p. 175
- 15' Body narrower, mandibles, pronotum and elytra not broadly explanate laterally; ligula with two setae; paraglossae glabrous *Lelis* Chaudoir, p. 174

"Thyreopteroids"

Within this group, *Phloeoxena* stands apart because of the distinctive microsculpture of its members: isodiametric plesiotypically, meshes keeled and arranged in longitudinal rows in the more apotypic forms. Probably this is the most plesiotypic genus in the New World. In the Old World, a number of thyreopterine genera such as *Thyreopterus*, *Eurydera* and *Labocephalus* exhibit isodiametric microsculpture on the elytra. The genera *Oreodicastes*, *Stenognathus*, *Ochropisus* and *Catascopus* share many character states, although it is doubtful if *Catascopus* is closely related to the other three.

Phloeoxena Chaudoir

In addition to the characteristics presented in the key, the members of this genus are recognized by a combination of: pronotum subcordate; mentum with lateral lobes acute apically; male with single pair of setae on abdominal sternum VII. Adults of this genus are illustrated in Fig. 16-19.

The group whose members most closely resemble those of *Phloeoxena* is *Ochropisus*. They share the following characteristics: mental tooth present; mental lobes acute at apex; and male with single pair of setae on abdominal sternum VII. In addition, males of the subgenera *Tacana* and *Oenaphelox* share with those of *Ochropisus* absence of modifications of the front femora, and the specimens of *Tacana* are glabrous ventrally, like those of *Ochropisus*. However, it is not clear which, if any, of these shared characteristics are apotypic. Consequently, a close relationship between these two genera has not been demonstrated.

For details, see the following section, pages 178-238.

Oreodicastes Maindron

Oxyglossus Chaudoir, 1843: 424 (NOT Swainson, 1827; NOT Tschudi, 1838). — Lacordaire, 1854: 258. — Chaudoir, 1869a: 114. — Maindron, 1905: 95. — Csiki, 1932: 766. TYPE

SPECIES (by monotypy) . — *Oxyglossus subcyaneus* Chaudoir, 1843: 424.

Oreodicastes Maindron, 1905: 95. — 1906: 195. — Csiki, 1932: 766 and 1352. — Blackwelder,



Fig. 16-19. Photographs of dorsal aspect of representative New World pericalines. Fig. 16. *Phloeoxena* (*Oenaphelox*) *undata* Chaudoir: Length 7.3 mm. Fig. 17. *Phloeoxena* (*Oenaphelox*) *geniculata* Chaudoir: Length, 6.3 mm. Fig. 18. *Phloeoxena* (*Tacana*) *herculeano*, new species: Length, 13.4 mm. Fig. 19. *Phloeoxena* (*sensu stricto*) *picta unicolor* Chaudoir: Length 10.0 mm. NOTE: "Length" includes mandibles, head, from mandibular articulation to behind compound eye; length of pronotum along mid-line, and length of longer elytron from basal groove to apex, measured in straight line.



20



21



22



23



24



25

Fig. 20-25. Photographs of dorsal aspect of representative New World pericalines. Fig. 20. *Oreodicastes subcyaneus* Chaudoir: Length 14.1 mm. Fig. 21. *Stenognathus (sensu stricto) quadricollis* Chaudoir: Length, 19.1 mm. Fig. 22. *S. (Pristolomus) dentifer* Chaudoir: Length, 18.3 mm. Fig. 23. *S. (Phloeotherates) chaudiroidi*, new name: Length, 14.6 mm. Fig. 24. *Ochropisus concolor*, new species: Length 7.1 mm. Fig. 25. *Catascopus chontalensis* Bates: Length 15.3 mm. NOTE: Measurements summed to give "Length" are indicated in the captions of Fig. 16-19.

1944: 41.

Note on nomenclature. — Maindron (1905) pointed out that *Oxyglossus* Chaudoir was a junior homonym of *Oxyglossus* Swainson, and proposed as replacement *Oreodicastes*, which takes the same type species as that of *Oxyglossus* Chaudoir.

Recognition. — An additional characteristic for recognition of this group is the tarsal claws with pectination confined to the basal areas.

The dark coloration of the dorsal surface and transverse microsculpture of the elytra with very wide meshes, form of the mentum, ligula and paraglossae (Fig. 26 cf. Fig. 29 and 34) suggest close relationship with *Stenognathus*.

Description. — Form agonoid (Fig. 20), moderately convex, not depressed. Size moderate (standardized body length ca. 10 mm).

Color. Black, antennae, palpi and tarsi rufous.

Microsculpture. Head, dorsum, meshes isodiametric. Pronotum, meshes transverse. Pteropleura, meshes isodiametric; pterosterna, meshes isodiametric laterally, transverse medially. Elytra, meshes transverse.

Luster. Generally shining, areas with transverse or longitudinal microsculpture meshes, iridescent.

Head. Eyes, smaller than average for Pericalina (Fig. 20).

Mouthparts. Generally as described for Pericalina. Labium (Fig. 26): mentum toothed, lobes moderately long (M: 1/w 0.44), narrowly truncate apically; ligula narrowed apically, quadrisetose, middle pair of setae longer than lateral ones; paraglossae subequal in length to ligula, asetose.

Prothorax. Pronotum as in Fig. 27, width greater than 0.66 width elytra at humeri; convex medially, transverse; anterior margin moderately concave, basal margin subtruncate; anterior angles prominent, narrowly rounded; posterior angles broadly rounded; sides reflexed, margins beaded; surface smooth; asetose. Prosternum asetose.

Pterothorax. Metepisternum subquadrate, anterior and lateral margin subequal in length; metasternum and middle coxal cavity subequal in length. Pterosterna asetose.

Elytra. Humeri broadly rounded, sides rounded, slightly explanate, narrowly reflexed; apical margin oblique, agonine-like, markedly sinuate, apex acute. Scutellar stria obsolete. Striae 1-8 deep. Intervals convex.

Hind wings. Short stubs.

Legs. Not especially slender or long, hind tarsus clearly shorter than hind tibia. Anterior femur of male without patch of setae ventrally. Middle and hind tibiae with dorsal surfaces rounded, smooth. Hind basitarsus not elongate, less than twice length of article 2. Tarsal claws each with about five pectinations, row short, confined to basal half.

Abdomen. Sterna glabrous, except ambulatory setae. Both sexes with four apical setae.

Male genitalia. Median lobe as in Fig. 28 A and B, anopic, apical orifice inclined to left, apical portion narrow, triangular, small. Internal sac with apical ring sclerite.

Ovipositor. Average for Pericalina.

Notes. — This genus includes two species, known only from Brazil. Originally described as an "anchomenide", Chaudoir later transferred it to the thyreopterides. Maindron returned it to the agonines, followed by Blackwelder, but Csiki treated *Oreodicastes* as a lebiine, including in that group the Thyreopterides of Chaudoir.

Stenognathus Chaudoir

Literature citations and synonymical notes are provided below, in conjunction with treatment of each subgenus.

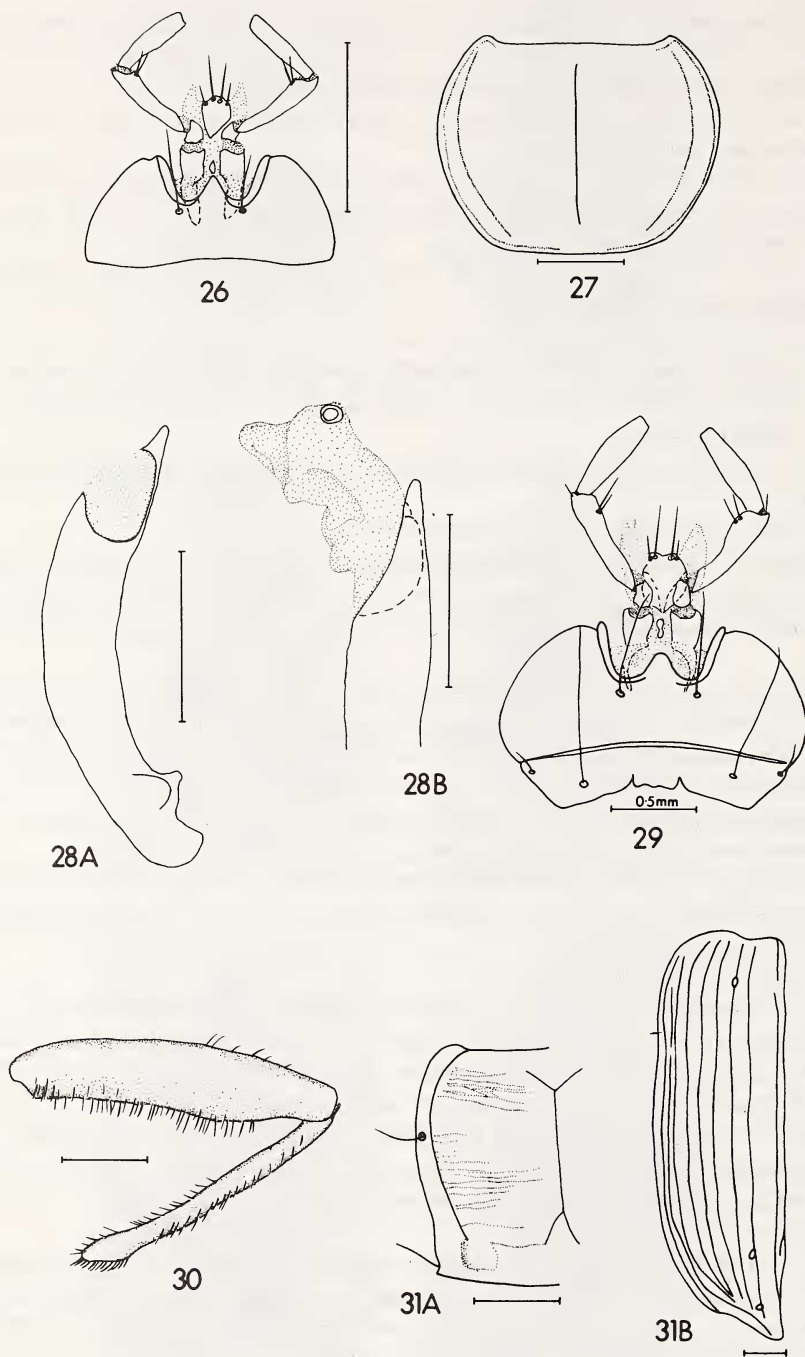


Fig. 26-28. *Oreodicastes subcyaneus* Chaudoir. Fig. 26. Labium, ventral aspect. Fig. 27. pronotum, dorsal aspect. Fig. 28. male genitalia, median lobe: A, left lateral aspect; B, apical portion, ventral aspect. Fig. 29-31. *Stenognathus* (*sensu stricto*) *quadricollis* Chaudoir. Fig. 29. Labium, ventral aspect. Fig. 30. left femur and tibia, anterior aspect. Fig. 31. A, pronotum, left half; B, left elytron, dorsal aspect.

Additional characteristics for recognition of this genus are: size moderate; elytral microsculpture transverse, with very long meshes; mentum with lateral lobes more or less broadly rounded; disc of pronotum strigulose; elytra with striae impunctate, and intervals moderately convex; and males with more or less densely setose femora, ventrally.

The members of this genus most closely resemble those of *Ochropisus*, and the two are probably closely related.

The three groups included as subgenera of *Stenognathus* were described by Chaudoir as distinct genera. However, their differences are so outweighed by their similarities it is clear that they are very closely related.

Description. — Form rather broad (Fig. 21-23), deplanate or moderately convex. Size moderate. (Standardized body length 9.5-12.5 mm).

Color. Generally black to piceous; antennae, palpi and legs rufopiceous.

Microsculpture. Head, dorsum, meshes isodiametric, or lines very fine, meshes not formed; venter, lines fine, meshes transverse or isodiametric. Pronotum, meshes transverse. Pteropleura and pterosterna, meshes isodiametric or transverse. Elytra, meshes transverse.

Luster. Generally shining; pronotum iridescent, elytra not so; ventral surface, generally iridescent.

Head. Eyes, average for Pericalina.

Mouthparts. Generally, as described for subtribe. Labium (Fig. 29, 34): mentum toothed, lobes long (M: 1/w 0.41-0.45), broadly rounded apically; ligula quadrisetose, broad or narrow apically; paraglossae distinctly longer than ligula, asetose, narrowed or not apically.

Prothorax. Pronotum as in Fig. 21-23, 31, decidedly narrower than elytra at humeri; surface distinctly transversely strigulose; slightly convex medially; anterior margin moderately concave, basal margin truncate; lateral margins sinuate basally; anterior angles narrowly rounded; posterior angles slightly obtuse or rectangular; sides slightly reflexed, margins not beaded; lateral setae, anterior pair inserted submarginally, posterior pair inserted on margins. Prosternum setose apically, more so in males than in females.

Pterothorax. Metepisternum longer than wide, metasternum longer than middle coxal cavity. Metasternum and antecoxal piece setose, more so in males than in females.

Elytra. Humeri broadly rounded; sides slightly rounded, lateral margins slightly explanate, not reflexed, serrulate or not; apical margin subtruncate, markedly sinuate, preapical angle toothed or not; apical angle narrowly rounded or toothed. Striae well developed. Intervals more or less convex.

Hind wings. Normal, evidently functional for flight.

Legs. Not especially slender or long, hind tarsus clearly shorter than hind tibia. Middle and hind coxae and trochanters more or less densely setose in males, or sparsely setose in females; femora with numerous extra setae in males, few in females. Middle and hind tibiae with dorsal surfaces rounded, not canaliculate, smooth or strigulose. Hind basitarsus not elongate, less than twice length of article 2. Tarsal articles slightly depressed, each with pair of setae dorso-apically; hind basitarsus with few additional setae dorsally. Tarsal claws pectinate or not.

Abdomen. Sterna III, IV and V medially more or less densely setose in males, sparsely setose in females. Sternum VII with apical setae four in both sexes.

Male genitalia. As in Fig. 32, 35 and 37: anopic, apical orifice moderate to small, inclined on left side; internal sac with apical ring sclerite.

Ovipositor. Fig. 33 and 36: as described for Pericalina.

Subgenus *Stenognathus* (*sensu stricto*)

Stenognathus Chaudoir, 1843: 431. — Lacordaire, 1854: 358. — Chaudoir, 1869a: 115. —

Bates, 1883: 175. — Csiki, 1932: 1352. — Blackwelder, 1944: 57. TYPE SPECIES (by monotypy). — *Anchomenus melanarius* Dejean, 1831: 718.

Distinguishing features are presented in the key.

Description. — Form as in Fig. 21. Labium as in Fig. 29. Pronotum as in Fig. 31. Left femur and tibia, as in Fig. 30. Distinctive features are: head, dorsum, shining, meshes not formed by lines of microsculpture; width of pronotum about 0.66 width of elytral humeri; elytron with lateral margin smooth, not serrulate, without tooth at preapical angle, apical angle with tooth; tarsal claws smooth, not pectinate; middle and hind tibiae with dorsal surfaces strigulose; males with middle and hind coxae, trochanters and femora ventrally, densely setose; sterna III, IV, V and VI setose; median lobe less curved than in *Phloeotherates*, apical orifice smaller, apical portion larger (Fig. 32 A and B; cf. Fig. 37 A and B). Ovipositor, coxite and stylus as in Fig. 33.

Notes. — This subgenus includes nine species, whose aggregate range extends from northern South America to southeastern Mexico. One of the two Middle American species (*S. quadricollis* Chaud.) ranges from Panama to southeastern Mexico.

Subgenus *Pristolomus* Chaudoir

Pristolomus Chaudoir, 1869a: 128. — Csiki, 1932: 1355. — Blackwelder, 1944: 57. TYPE SPECIES (by monotypy). — *Pristolomus dentifer* Chaudoir, 1869a: 128.

Description. — Form as in Fig. 22. Labium as in Fig. 34. Distinctive features are: head, dorsum, dull, meshes of microsculpture distinct, isodiametric; elytron with lateral margin serrulate, preapical and apical angles dentate; tarsal claws not pectinate; middle and hind tibiae with dorsal surfaces strigulose; middle and hind coxae and trochanters, front, middle and hind femora ventrally, densely setose; abdominal sterna III and IV sparsely setose; median lobe almost straight, apical orifice small, apical portion in ventral aspect narrower than in *Stenognathus* (Fig. 35 A and B). Ovipositor, coxite and stylus as in Fig. 36.

Notes. — The single included species, *Stenognathus dentifer* Chaudoir, is known only from Colombia.

Subgenus *Phloeotherates* Bates

Phloeotherates Bates, 1869: 71, 79. — 1870: xvii. — 1883: 175-176. — Maindron, 1906: 195-202. — Csiki, 1932: 1353. — Blackwelder, 1944: 57. — TYPE SPECIES (by monotypy).

— *Phloeotherates nigropiceus* Bates, 1869: 80.

Ferus Chaudoir, 1869a: 119. — Bates, 1870: xvi. — Csiki, 1932: 1353. — Blackwelder, 1944: 57. TYPE SPECIES (here designated). — *Ferus quadricollis* Chaudoir, 1869: 119. (= *Stenognathus chaudiroidi* new name).

Notes on nomenclature. — The names *Phloeotherates* and *Ferus* were proposed in the same year for the same genus. Bates and those who followed him chose to use the former name, and I accept this. Because this group is here combined with *Stenognathus*, the name *Phloeotherates quadricollis* Chaudoir, 1869 becomes a junior subjective homonym of *Stenognathus quadricollis* Chaudoir, 1843. To replace the former, I choose here *Stenognathus chaudiroidi*, new name.

Description. — Form as in Fig. 23. Distinctive features are: head, dorsum shining, meshes not formed by lines of microsculpture; pronotum more than 0.66 width of humeri; elytra with lateral margins smooth, without tooth at preapical angle, apical angle broadly rounded; tarsal claws pectinate; middle and hind tibiae with dorsal surfaces smooth, not strigulose; males with middle and hind coxae and trochanters sparsely setose, middle femur with numerous setae

ventrally; abdominal sterna III, IV, V and VI moderately densely setose; median lobe markedly curved, short, apical portion very short, and apical orifice large (Fig. 37 A, B and C).

Notes. — Maindron (1906) provides a key to the six species of this subgenus, whose range extends from northern South America to southeastern Mexico. The range of the single species entering Mexico, *S. chaudiroidi*, extends southward to Panama. Adults of this species have been collected from under bark of logs, in the company of adults of several species of *Coptodera*, in tropical montane forest, at an elevation of about 3500 feet above sea level.

Ochropisus Bates

Ochropisus Bates, 1883: 176. — Csiki, 1932: 1353. — Blackwelder, 1944: 57. — TYPE SPECIES (here designated). — *Ochropisus caudalis* Bates, 1883: 176.

Characteristics for recognition additional to the ones presented in the key are: small size; mentum with lobes acute at apex; pronotum transverse, with base and apex subequal, and base sublobate; lateral grooves irregularly and coarsely punctate; male with single pair of setae on abdominal sternum VII and median lobe catopic.

In size and in possession of a basal lobe on the pronotum, members of this group are most like those of *Stenoglossa* Chaudoir, but the two are easily separated by the characters presented in the key. Probably *Ochropisus* is most closely related to *Stenognathus*, possibly to the subgenus *Phloeotherates*.

Description. — Form as in Fig. 24, rather broad. Size small (standardized body length ca. 3.5-5.0 mm).

Color. Body rufopiceous, elytra uniform rufopiceous, or bicolored with apices flavous. Antennae, mandibles, palpi and legs rufoflavous.

Microsculpture. Head, dorsum, meshes isodiametric. Pronotum and prosternum, meshes transverse; propleura, meshes longitudinal. Elytra, meshes transverse.

Luster. Dorsal surface shining, elytra faintly iridescent or not; ventral surface shining, abdominal sterna and propisterna faintly iridescent.

Head. Ventral surface without transverse depression behind eyes, latter smaller and flatter than average.

Mouthparts. Generally as described for subtribe. Labium (Fig. 38 A and B): mentum toothed, lateral lobes acute apically, long (M: 1/w 0.42); ligula narrowed apically, quadrisetose; paraglossae glabrous, subequal in length to ligula.

Prothorax. Pronotum as in Fig. 24, width more than 0.66 width of elytra at humeri; slightly convex, surface transversely strigulose, lines very fine; anterior margin shallowly concave, posterior margin slightly lobed medially; laterally sloped obliquely forward; anterior angles broadly rounded; posterior angles rectangular; sides slightly reflexed, not beaded slightly sinuate or not, posteriorly; setae inserted on lateral margins. Prosternum glabrous.

Pterothorax. Metepisternum longer than wide. Metasternum medially longer than middle coxal cavity, glabrous.

Elytra. Humeri broadly rounded, sides subparallel, very slightly reflexed, not explanate, apical margins subtruncate, feebly sinuate; apical angles about rectangular, preapical angles broadly rounded. Striae punctate, shallow but distinctly impressed. Intervals almost flat.

Hind wings. Normal, evidently functional as flight organs.

Legs. Moderately long, hind tarsus subequal in length to hind tibia. Femora without extra setae, middle and hind tibiae each with dorsal surfaces longitudinally canaliculate. Hind basitarsus less than twice length of article 2. Tarsal articles dorsally each with single pair of setae near apex. Tarsal claws each with pectinations beyond middle.

Abdomen. Sternum VII with apical setae two in male, four in female.

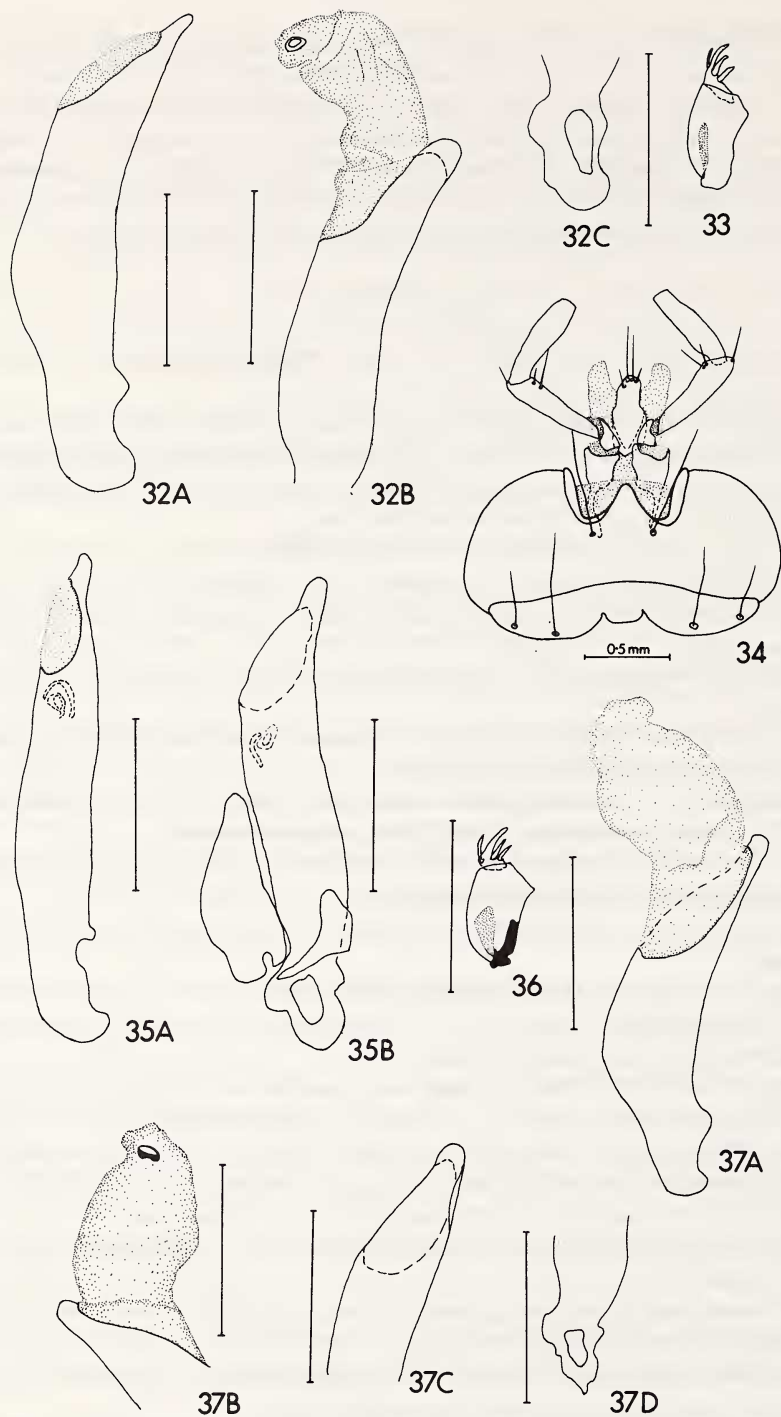


Fig. 32-33. *Stenognathus (sensu stricto) quadricollis* Chaudoir. Fig. 32. male genitalia: A, left lateral aspect; B, apical portion, ventral aspect; basal portion, ventral aspect. Fig. 33. ovipositor, coxite and stylus, ventral aspect. Fig. 34-36. *Stenognathus (Pristolomus) dentifer* Chaudoir. Fig. 34. labium, ventral aspect. Fig. 35. male genitalia: A, median lobe, left lateral aspect; B, median lobe, apical portion, ventral aspect. Fig. 36. ovipositor: coxite and stylus. Fig. 37. *Stenognathus (Phloeotherates) chaudoiri*, new name. Fig. 37. male genitalia, median lobe: A, left lateral aspect; B, right lateral aspect, internal sac everted; C, apical portion, ventral aspect; D, basal portion, ventral aspect.

Male genitalia. As in Fig. 39 A-B. Median lobe catopic; apical orifice small, left-ventral in position.

Ovipositor. Average for Pericalina (Fig. 40, coxite and stylus).

Notes. — The range of this genus extends in Middle America from Panama to central Mexico. Three species are included, one of which is described as new. Adults are distinguished from one another in the following key.

Key to Species of *Ochropisus* Bates

- 1 Elytron bicolored, with flavous apical fascia and pale rufous humeral spot; intervals flat; standardized body length various; known range, south of Mexico 2
- 1' Elytron concolorous; intervals feebly convex; standardized body length larger, about 4.5 mm, or more *Ochropisus concolor*, new species, p. 165
- 2 Standardized body length greater than 4.5 mm *Ochropisus caudalis* Bates
- 2' Standardized body length less than 4.5 mm *Ochropisus bembidioides* Bates

Ochropisus concolor, new species

The diagnostic combination of characteristics is indicated in the preceding key.

Description. — Form as in Fig. 24. Data on variation in the following measurements and ratios are presented in Table 1: standardized body length; Hw/Pwm; Hw/P1; P: Aw/Bw; P: 1/w.

Table 1. Data on Variation in Selected Measurements and Ratios within a Population Sample of *Ochropisus concolor*, New Species, from the Vicinity of Cuernavaca, Mexico.

Character	Males N = 7		Females N = 5	
	Range	Mean	Range	Mean
SBL (mm)	4.40 - 5.00	4.820	4.62 - 4.90	4.770
Hw/Pwm	0.771 - 0.810	0.794	0.770 - 0.810	0.793
P: 1/w	0.680 - 0.755	0.718	0.700 - 0.760	0.728
P: Aw/Bw	0.750 - 0.800	0.774	0.750 - 0.800	0.778

Color. Dorsal surface rufopiceous, head and disc of pronotum slightly darker than lateral margins of pronotum and elytra, latter with epipleura and lateral margins flavous.

Pronotum with sides faintly but distinctly sinuate in front of hind angles.

Elytra with striae distinctly punctate; intervals more convex, and in basal half sparsely but more distinctly punctulate than in adults of other species of *Ochropisus*.

Male genitalia, median lobe as in Fig. 39 A-B.

Type material. — HOLOTYPE male and ALLOTYPE female labelled: MEX. Morelos, 9.1 mi. e. Cuernavaca, 4300', Cañon de Lobos, XI.25.65, George E. Ball and D. R. Whitehead. PARATYPES, six males, four females; four males, one female labelled like holotype; two males, three females labelled MEX. Morelos, 7 kil. e. Cuernavaca, 5800', August 11, 1962, H. E. Evans Exp., George E. Ball.

Disposition of type material. — The holotype and allotype are in USNM. Paratypes are in: BMNH, CAS, CNC, IPNM, MCZ, MNHP, UASM.

Derivation of the specific epithet. — Latin, meaning same color; in allusion to the approximately uniform color of the elytra.

Notes on habitat. — The beetles were taken from trees by beating leaves and branches which

were either partly or wholly dead. The forest located 7 kil. east of Cuernavaca was the Balsas drainage thorn forest, a dry tropical semi-deciduous forest, growing on an old lava field, or pedregal. It was difficult to move around, both because of the dense spiny vegetation and the very uneven surface of the ground.

Cañon de Lobos is a narrow steep-sided ravine with water in the bottom during the rainy season. The soil is clay, on limestone rock, and becomes very dry. The trees form a rather open canopy, and many of the lower branches are within easy reach of a person standing on the ground. This was one of the few places in Mexico that we were able to obtain a quantity of beetles by scaling off loose bark with knives.

In addition to specimens of this species, we also obtained under bark in the same area adults of *Phloeoxena* (*Oenaphelox*) *geniculata* Chaudoir.

Catascopus Kirby

Catascopus Kirby, 1825: 94. — Dejean, 1825: 328. — Lacordaire, 1845: 145. — Bates, 1869: 72. — Chaudoir, 1869a: 158. — Bates, 1883: 178. — Csiki, 1932: 1362. — Blackwelder, 1944: 57. — Jeannel, 1949: 1007. — Habu, 1967: 77. — Darlington, 1968: 101. — 1971: 194. — Reichardt, 1972: 238. TYPE SPECIES. — *Catascopus hardwickii* Kirby, 1825.

Subgenus *Catascopus* (*sensu latissime*)

Additional characteristics for recognizing New World members are: mentum with blunt tooth; ligula with outer pair of setae longer than inner pair; pronotum with both pairs of setae marginal; elytra with striae shallow, punctate; and males with oval patch of setae baso-ventrally, on front femora.

The following additional features distinguish these species from their Old World counterparts: left mandible without terebral tooth; submentum quadrisetose; elytron with all intervals flat, not carinate, preapical and apical angles not spined, umbilicate series with penultimate puncture clearly not aligned with the ante-penultimate and ultimate punctures; and male with ventral surface not densely hairy.

The characteristics of this group are most like those of *Stenognathus*, but most of the similarities may be symplesiotypic, so relationships are uncertain. Features shared by members of *Stenognathus* and the Old World members of *Catascopus* are: strigulose dorsal surfaces of the middle and hind tibiae; and males with ventral surface more setulose than females.

With members of *Ochropisus* the New World members of *Catascopus* share shallow, punctate elytral striae and canaliculate tibiae. However, the two groups differ in many characteristics, so it is unlikely that these similarities are of much significance as indicators of relationship.

Notes on classification. — Habu (1967: 78) began the process of classifying the species of *Catascopus* when he erected the monotypic subgenus *Catascopidius*. That, however, was not much of a contribution for it left behind a vast paraphyletic assemblage in the nominotypical subgenus. According to Basilewsky (1953: 208) the New World species currently assigned to this genus should be placed in a genus of their own. I agree that they form a distinct group, based on the combination of characteristics listed above. cursory examination of a limited sample of Old World material (ten species, including the type species, from Africa, India, Java, Borneo, the Philippines and New Guinea) satisfies me that this group is sufficiently divergent to encompass the New World species, and that both groups share enough apotypic character states to indicate close relationship. Therefore, I am not inclined to separate these two geographical groups at the generic level. Nor am I inclined to follow Habu's example and erect a separate subgenus for the New World species. That should be done, I think, in the course of

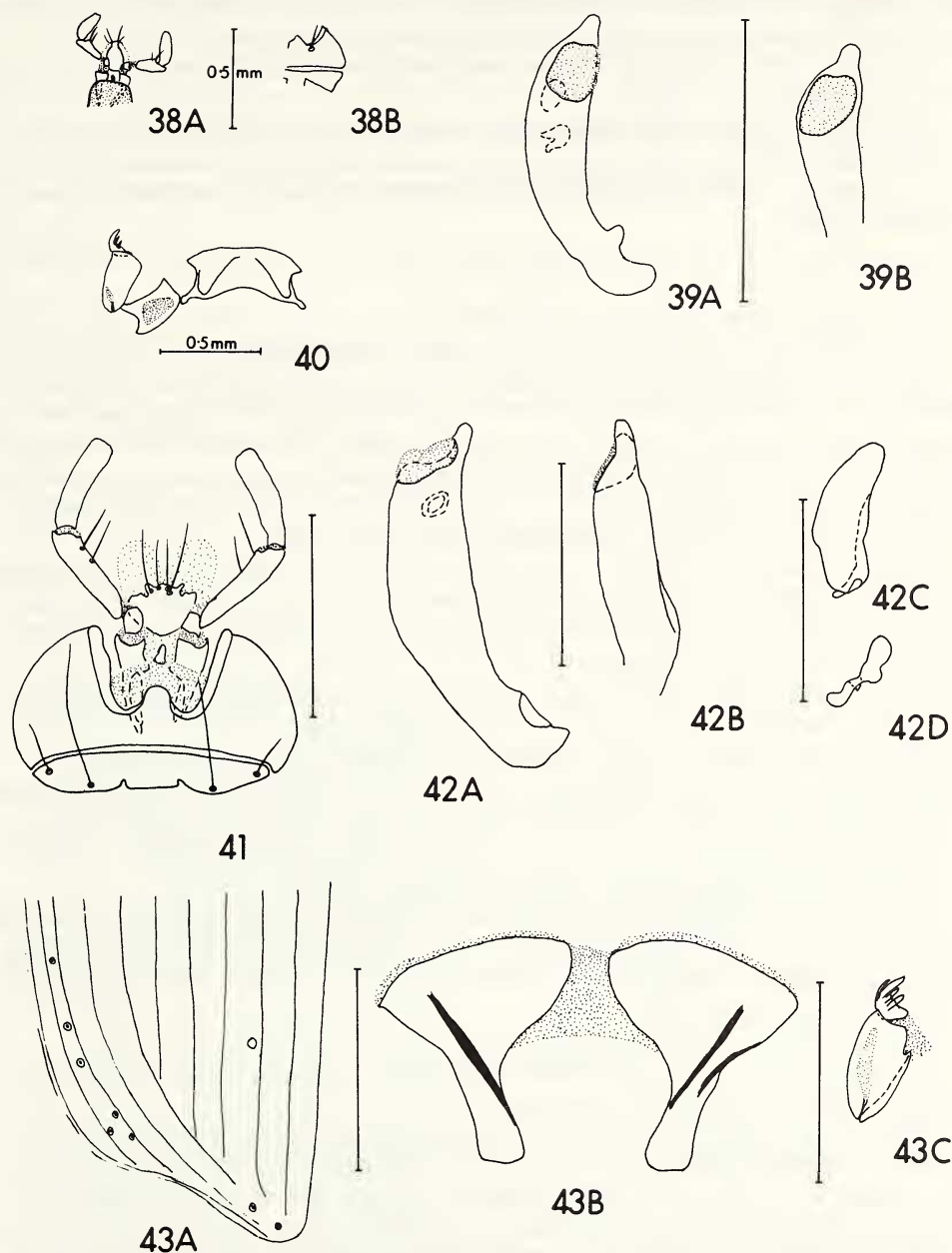


Fig. 38-40. *Ochropis concolor*, new species. Fig. 38, Labium, ventral aspect: A, Ligula, paraglossae, and palpi; B, Mentum. Fig. 39. Male genitalia, median lobe: A, left lateral aspect; B, ventral aspect. Fig. 40. Ovipositor, tergum X, valvifer, coxite and stylus. Fig. 41-43. *Catascopus*. Fig. 41. Labium, ventral aspect. Fig. 42. Male genitalia: A, median lobe, left lateral aspect; B, median lobe, ventral aspect; C, left paramere; D, right paramere. Fig. 43A. Left elytron. Fig. 43B. Tergum VIII. Fig. 43C. Ovipositor: coxite and stylus. (Fig. 43A, of *C. validus* Chaudoir; others, of *C. chontalensis* Bates).

a study of classification of the entire genus — a task which would be delightful and challenging. My opinion is that the New World group of species is the plesiotypic sister group of the much more diverse and divergent complex of species inhabiting the Old World.

Description (American species). — Form moderately slender (Fig. 25), size moderate (standardized body length ca. 10 mm).

Color. Dorsum metallic green. Ventral surface and appendages piceous to rufopiceous.

Microsculpture. Head, dorsum, lines very fine, meshes not formed. Pronotum meshes transverse; pteropleura, meshes isodiametric. Elytra, meshes transverse, in rows slightly diagonal to longitudinal axis.

Luster. Dorsal surface with head and pronotum shining, elytra rather dull. Ventral surface shining, not iridescent.

Head. Surface sparsely micropunctate. Frontal impressions deep, broad. Eyes, large, prominent, bulged (Fig. 25). Clypeus with anterior margin feebly emarginate.

Mouthparts. Generally average for *Pericalina*. Labrum nearly as long as wide, anterior margin deeply but narrowly notched. Maxillary stipes with two long setae laterally near base. Labium (Fig. 41): mentum toothed; lobes long each narrowly rounded or briefly subtruncate at apex (M: l/w 0.43); ligula broad apically, quadrisetose, lateral setae longer than medial ones, paraglossae longer than ligula, adnate to each other beyond ligula, each with apex broadly rounded; labial palpus with one seta near apex, one about 0.75 distance from base.

Prothorax. Pronotum as in Fig. 25, anterior margin broadly concave, basal margin truncate; anterior angles prominent, narrowly rounded, posterior angles narrowly obtuse; sides slightly reflexed, beaded anteriorly, markedly sinuate posteriorly; setae inserted on lateral margins. Prosternum sparsely setose medially.

Pterothorax. Metepisternum longer than wide. Metasternum longer than middle coxal cavity. Mesosternum and metasternum each with few setae medially.

Elytra. Humeri broadly rounded. Sides more or less parallel to one another, slightly explanate, not reflexed, apical margins feebly sinuate, apical and preapical angles broadly rounded. Striae shallow but distinct, punctate; intervals flat. Interval 3 with three to five setigerous punctures; interval 5 with or without one setigerous puncture in basal one-third.

Hind wings. Normally developed, evidently functional in flight.

Legs. Not long and slender, hind tarsus shorter than hind tibia. Anterior femur of male with small patch of short setae ventrally near base. Dorsal surfaces of middle and hind tibiae longitudinally canaliculate. Hind basitarsus less than twice length of article 2. Tarsal articles 1 and 2 with scattered setae dorsally.

Abdomen. Sternum VII with apical margin entire and quadrisetose in both sexes.

Male genitalia. As in Fig. 42 A-D; anopic, apical orifice small, dorsal; apical portion short, rounded. Internal sac with apical ring sclerite.

Ovipositor. Average for *Pericalina* (Fig. 43 B-C: tergum VIII; coxite and stylus).

Notes. — More than 100 species are included in this genus, the aggregate range including the tropics of the world, and the eastern portion of the Palaearctic Region northward to the Japanese Archipelago. Eight species are known from the New World, ranging from Brazil to northwestern Mexico. Six of these are confined to Middle America. Adults of the three species known from Mexico are distinguished in the following key.

Adults are found under bark of trees that are recently dead or dying, either vertical or horizontal in position. Members of this genus occur in the company of other pericalines, such as various species of *Coptodera*. Although adults of some Old World species of *Catascopus* are known to be diurnal, the time of activity of New World adults seems to be nocturnal.

Key to Adults of the Mexican Species of *Catascopus* Kirby

- 1 Elytron, interval 3 with four to five setigerous punctures; interval 5 with or without setigerous puncture near base *C. obscuriviridis* Chevrolat
- 1' Interval 3 of elytron with three discal setigerous punctures, interval 5 without setigerous puncture 2
- 2 (1') Pronotum with small denticle on margin, in association with anterior setigerous puncture *C. mexicanus* Chaudoir
- 2' Pronotum with lateral margin evenly rounded, not denticulate *C. chontalensis* Bates

"Somotrichoids"

Treatment of this group is cursory because, after the manuscript was thought to have been completed, the somotrichoids were added to the Pericalina, partly as a result of advice from Hans Reichardt, and partly as a result of an unexpected opportunity to study the collection of unidentified lebiines in the USNM.

The genus *Somotrichus* and several other African genera including pale colored setulose adults were grouped in the Tribe Singilini, subfamily Lebiinae by Jeannel (1949: 915). Mateu (1963) showed that the Singilini Jeannel was comprised of three distinct groups of genera, each of which he ranked as a tribe of the subfamily Lebiinae. He restricted the Singilini to include only *Singilis* Rambur. In the Lichnasthenini he placed *Lichnasthenus* Thomson, *Velindomimus* Jeannel, *Velindopsis* Burgeon, and *Microvelindopsis* Mateu. He erected the Somotrichini to include *Somotrichus* Seidlitz, *Pephrica* Alluaud, and *Paulianites* Jeannel. (Mateu did not refer to *Oecornis* Britton, 1940, although Jeannel (1949: 1126) transferred to it *Somotrichus vadoni* Jeannel. Probably *Oecornis* is a somotrichoid, but this is not yet established). It seems clear from the figures and descriptions published by Mateu that the genera included in the Somotrichini really are related to *Somotrichus*, and hence also belong in the subtribe Pericalina. It is also clear that the Singilini and Lichnasthenini belong elsewhere, probably in or near the subtribe Lebiina (*sensu* Habu, 1967).

With the somotrichoids I provisionally group *Catascopellus*. The general coincidence of diagnostic characteristics of this genus and the African somotrichoids suggest common ancestry, but the very large head and dark coloration of adults of *Catascopellus* set them apart. Nonetheless, this genus does not seem at all close to any other pericaline genus with which I am familiar.

Somotrichus Seidlitz

Somotrichus Seidlitz, 1887: 7. — Jeannel, 1949: 917. — Ball, 1960: 158. — Mateu, 1963: 131-133. — Habu, 1967: 74. — Darlington, 1968: 83. TYPE SPECIES. — *Carabus elevatus* Fabricius, 1792 (not *C. elevatus* Fabricius, 1787).

Note on nomenclature. — The valid name for the single included species is *Somotrichus unifasciatus* Dejean, 1831. The first proposed name, *Carabus elevatus* Fabricius, 1792 is a junior primary homonym of *Carabus elevatus* Fabricius, 1787 (= *Scaphinotus elevatus*), as Habu (1967: 75) wrote.

Identification. — See key, p. 155.

Description. — Form as in Fig. 43 E. Size small (standardized body length ca. 3.2-3.5 mm), integument generally setulose.

Color. Body generally testaceous; elytra bicolored with broad dark vitta (Fig. 43 E).

Microsculpture. Head, dorsum, meshes isodiametric; pronotum and pteropleura, meshes

transverse; elytra, meshes isodiametric, lines very fine.

Luster. Dorsal surface shining.

Head. Average for Pericalina. Eyes large, prominent, bulged (Fig. 43 E). Paragena narrower than antennal scape.

Mouthparts. Labrum wider than long (l/w 0.77), longer than clypeus (l. labrum/l. clypeus 0.50). Labium: mentum toothed, lobes long each with apex acute (M: l/w 0.50); ligula narrowed apically, bisetose; paraglossae subequal in length to ligula, broadly rounded; labial palpus with two long setae and several shorter ones.

Prothorax. Pronotum as in Fig. 43 E; anterior margin slightly concave; basal margin distinctly lobed medially; posterior angles rectangular; sides very slightly reflexed, sinuate posteriorly; lateral margins and lateral portions of anterior and posterior margins with each side with four or more long, thick setae.

Pterothorax. Metepisternum longer than wide. Metasternum longer than middle coxal cavity.

Elytra. Humeri broadly rounded. Sides parallel, not reflex or explanate; apical margin subtruncate, not sinuate; apical angles rectangular. Striae broad, shallow. Intervals feebly convex. Interval 3 with three discal setae.

Hind wings. Normally developed.

Legs. Not long and slender, hind tarsus shorter than hind tibia. Middle tibia of male with preapical notch in inner (ventral) margin. Dorsal surfaces of hind and middle tibiae rounded, not strigulose. Hind basitarsus almost twice length of article 2. Tarsal articles sparsely setose dorsally. Tarsal claws pectinate.

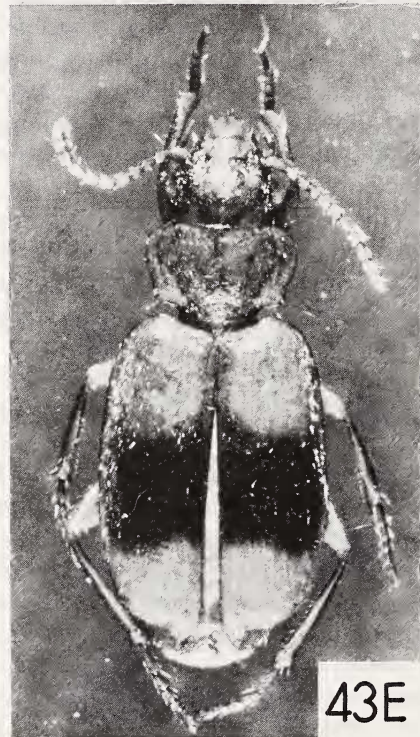


Fig. 43 D and E. Photographs of dorsal aspect of representative New World pericalines. Fig. 43 D. *Catascopellus crassiceps* Straneo: Length, 7.88 mm. Fig. 43 E. *Somotrichus unifasciatus* Dejean: Length, 3.72 mm. NOTE: Measurements summed to give "Length" are indicated in the captions of Fig. 16-19.

Abdomen. Sternum VII with single pair of setae.

Male genitalia. Anopic (Habu, 1967: Fig. 165).

Ovipositor. Average for Pericalina (Habu, 1967: Fig. 167).

Habits. — See section entitled "Notes on evolutionary trends", p. 153-155.

Catascopellus Straneo

Catascopellus Straneo, 1969: 972. TYPE SPECIES. — *Catascopellus crassiceps* Straneo, 1969. (Original designation).

See key, p. 155, for distinguishing characteristics.

Description. — Form as in Fig. 43 D, size small (standardized body length 5.84 mm). Dorsum sparsely setulose.

Color. Body piceous to black. Elytra dark green. Mouthparts and legs rufopiceous.

Microsculpture. Dorsum of head with meshes isodiametric, large. Pronotum, meshes transverse medially, isodiametric laterally. Pteropleura, meshes isodiametric to transverse. Elytra, meshes isodiametric.

Luster. Dorsal surface moderately shining to dull.

Head. Relatively enormous (Fig. 43 D), about as long as pronotum, frons irregularly sculptured. Temporal areas posterior to eyes swollen. Laterodorsal areas behind eyes setulose. Eyes reduced. Paragena width greater than width of antennal scape.

Mouthparts. Labrum elongate (l/w base 0.74), as long as clypeus. Labium toothed, lateral lobes long (M: l/w 0.42), each lobe acute apically; ligula, apical margin truncate, quadrisetose, lateral pair of setae longer than medial pair; paraglossae in length subequal to ligula.

Prothorax. Pronotum as in Fig. 43 D, sparsely setulose; anterior margin shallowly concave; posterior margin distinctly lobed medially; anterior angles broadly rounded, posterior angles obtuse, narrowly rounded; sides sinuate, reflexed. Marginal setae two or three pairs, anterior pair inserted submarginally. Prosternum sparsely setulose.

Pterothorax. Setulose. Metepisternum elongate. Metasternum longer than middle coxal cavity.

Elytra. Humeri broadly rounded. Sides parallel, margins slightly reflexed, not explanate; preapical margin sinuate; preapical and apical angles acute. Striae shallow, broad, shallowly punctate, each puncture with short seta. Intervals feebly convex, serially shallowly punctate, each puncture with very short seta. Interval 3 with three long tactile setae. Umbilical series 15 setae, more or less evenly spaced, penultimate setigerous puncture displaced laterally.

Hind wings. Normally developed.

Legs. Average. Dorsal surface of hind tibia rounded, not keeled or canaliculate. Middle tibia of male with preapical notch in ventral or inner surface. Tarsi with dorsal surfaces sparsely setose. Tarsal claws smooth, not pectinate.

Abdomen. Sternum VII quadrisetose. Male genitalia and ovipositor not studied.

Notes. — The above description is abbreviated, and is based in part on the more extensive original description, and in part on a single female (CHILE, Prov. Malleco, Cordillera de Nahuelbuta, 4300', Parque Nacional; USNM).

Geographical distribution. — This genus is known only from the province of Malleco, in the mountains of south-central Chile.

"Eurycoleoids"

This group of genera is confined to the New World. It is not certain that *Stenoglossa* belongs

here, but this seems like a reasonable allocation for the present. The plesiotypic microsculpture of the females plus the absence of marked explanation of the body indicates a basal position for this genus. Also, the habits of adults seem to be plesiotypic, living as they do, on the outer surface of tree bark. From such a stock it is a considerable distance to the moderately explanate adults of *Leilis*, whose members are associated with fungi beneath the bark of dead logs. From the structural plan of *Leilis* it is a rather short step to the remarkable *Eurycoleus*, whose adults are characterized by a markedly flattened body, and both larvae and adults are associated with fungi, under bark (Erwin, personal communication).

Stenoglossa Chaudoir

Stenoglossa Chaudoir, 1848: 116. — Lacordaire, 1854: 141. — Chaudoir, 1869a: 201. — Bates, 1869: 71, 77. — Bates, 1883: 184. — Csiki, 1932: 1375. — Blackwelder, 1944: 58. — TYPE SPECIES (by monotypy). — *Stenoglossa variegata* Chaudoir, 1848.

The very small size of individuals of this genus, pale elytra with thin transverse markings and elongate labrum are additional features to aid in recognition of adults. The elongate basitarsus may be an additional indicator of relationships to *Leilis* and *Eurycoleus*.

Description. — Form as in Fig. 44, size very small (standardized body length about 2.5-3.5 mm).

Color. Variegated, infuscated to flavous. Head dark, pronotum dark with pale margins, elytra more or less predominantly pale with transverse dark markings.

Microsculpture. Head, dorsum, meshes isodiametric, large. Pronotum, meshes transverse. Pteropleura, meshes transverse. Elytra, meshes transverse or isodiametric.

Luster. Dorsal surface more or less shining, pronotum slightly iridescent.

Head. Venter without transverse impression behind eyes, latter large, bulged.

Mouthparts. Labrum (Fig. 48) almost as long as wide. Labium (Fig. 49 A and B): not toothed, lateral lobes long (M: l/w 0.41), each acute apically; ligula bisetose, narrow apically; paraglossae subequal in length to ligula.

Prothorax. Pronotum as in Fig. 44, maximum width more than 0.66 width of elytra at humeri; anterior margin shallowly concave; posterior margin distinctly and angularly lobate; anterior angles broadly rounded, posterior angles acute, sides reflexed, sinuate posteriorly; setae two pairs, anterior pair inserted submarginally. Prosternum glabrous.

Pterothorax. Glabrous.

Elytra. Sides rounded, reflexed, explanate; apical angle narrowly rounded, preapical angle broadly rounded. Striae shallow, intervals slightly convex.

Legs. Elongate, slender, hind tarsus subequal in length to hind tibia. Dorsal surface of hind tibia not keeled or canaliculate. Hind basitarsus elongate, more than twice length of article 2. Tarsal articles sparsely setose dorsally.

Abdomen. Male with dense patch of setae postero-medially on sternum IV; sternum VII more or less deeply and broadly notched in males (Fig. 50), entire in female, quadrisetose in both sexes.

Male genitalia. As in Fig. 51 A and B; anopic, apical orifice moderately large, inclined on left side; apical portion very short.

Ovipositor. Stylus as in *Coptodera*: subcylindrical, elongate, as in Fig. 52.

Notes. — This is an endemic New World genus, with eight described species whose aggregate range extends from Brazil and Colombia to central Mexico. The Middle American fauna includes only two wide-ranging species, one of which, *S. lineata* Bates, reaches Mexico. Adults are found on trees, living or dead, with loose, scaly bark, and in bromeliads.



Fig. 44-47. Photographs of dorsal aspect of representative New World pericalines. Fig. 44. *Stenoglossa lineata* Bates. Length 4.0 mm. Fig. 45. *Leilis insculpta* Bates. Length 9.5 mm. Fig. 46. *Eurycoleus macularis* Chaudoir. Length 11.5 mm. Fig. 47. *Coptodera elongata* Chaudoir. Length 12.1 mm. NOTE: Measurements summed to give "Length" are indicated in the captions of Fig. 16-19.

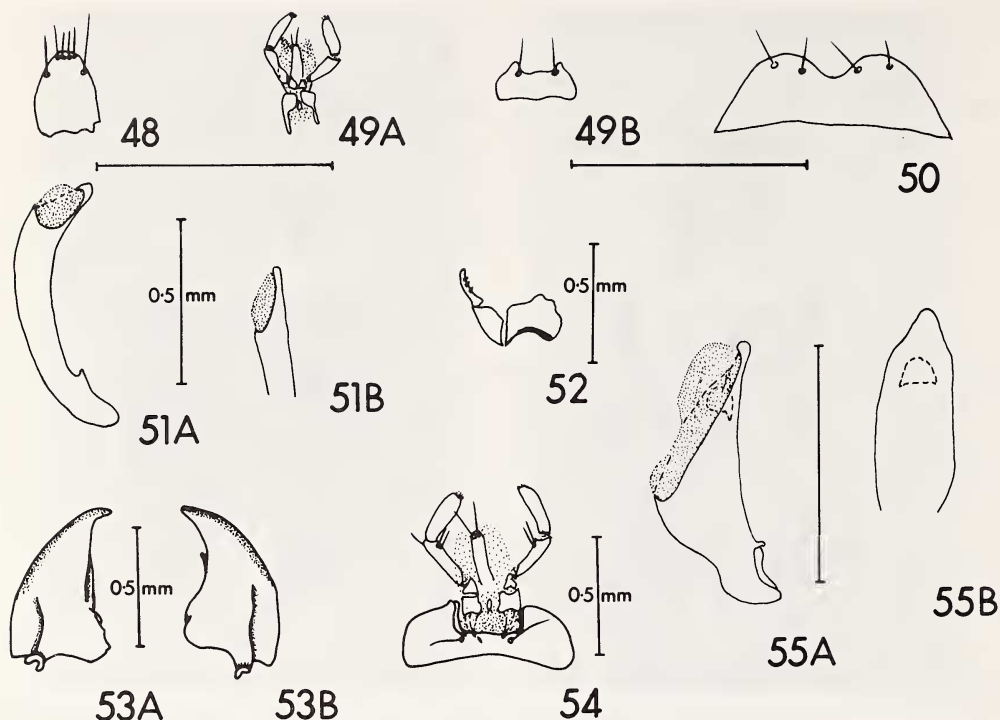


Fig. 48-52. *Stenoglossa lineata* Bates. Fig. 48. Labrum, dorsal aspect. Fig. 49. Labium, ventral aspect: A, ligula, paraglossae and palpi; B, mentum. Fig. 50. Sternum VII, male, ventral aspect. Fig. 51. Male genitalia, median lobe: A, left lateral aspect; B, ventral aspect. Fig. 52. Ovipositor: coxite and stylus, ventral aspect. Fig. 53-55. *Lelis insculpta* Bates. Fig. 53. Mandibles, dorsal aspect: A, left; B, right. Fig. 54. Labium, ventral aspect. Fig. 55. Male genitalia, median lobe: A, left lateral aspect; B, ventral aspect.

Lelis Chaudoir

Lelis Chaudoir, 1869b: 231. — Bates, 1883: 185. — Csiki, 1932: 1381. — Blackwelder, 1944: 58. — Reichardt, 1972: 238. TYPE SPECIES (here designated). — *Lelis bicolor* Chaudoir, 1869.

The characteristics presented in the key are sufficient to distinguish members of this genus from other pericalines.

The moderately explanate mandibles, short mental lobes, broad pronotum, elongate basitarsus, median lobe with large apical orifice and internal sac with broad apical plate are features which seem to indicate a close relationship between the members of *Lelis* and *Eurycoleus*.

Description. — Form quite broad, *Lebia*-like (Fig. 45). Size small (standardized body length 5.4-6.4 mm).

Color. Various: dorsum uniformly dark or bicolored, with head and pronotum rufous, elytra metallic green, or fasciate, with reddish brown and flavous markings. Antennae, mouthparts and legs rufous.

Microsculpture. Lines very fine on head and prothorax, coarser on elytra. Head, dorsum, meshes isodiametric. Pronotum, meshes transverse. Pteropleura and pterosterna, lines vermiculate, meshes not formed. Elytra, meshes transverse.

Luster. Generally shining, sterna iridescent.

Head. Frontal impressions broad, moderately deep, straight. Eyes, prominent, bulged.

Mouthparts. Mandibles (Fig. 53) explanate basally, less markedly so than in *Eurycoleus*, ventral margin clearly laterad of dorso-lateral margin, scrobe shallow, broad. Labium (Fig. 54): mentum edentate, lateral lobes shorter than average (M: l/w 0.33), each lobe broad, obliquely truncate at apex; ligula slender and bisetose apically; paraglossae glabrous, subequal in length to ligula.

Prothorax. Pronotum, as in Fig. 45, transverse, anterior margin moderately deeply concave, posterior margin sinuate to truncate medially, laterally sloped obliquely forward; anterior angles very broadly rounded; posterior angles obtuse; sides reflexed, not beaded; surface smooth; setae inserted on lateral margins. Prosternum, intercoxal process very sparsely setose.

Pterothorax. Pterosterna very sparsely setose.

Elytra. Sides rounded, subparallel, slightly reflexed laterally; apical margin markedly sinuate, preapical and apical angles feebly dentate. Striae clearly impressed, intervals feebly convex.

Legs. Not especially long and slender, hind tarsus shorter than hind tibia. Anterior femur of male without accessory setae. Hind tibia with dorsal surface rounded, not canaliculate or keeled. Hind basitarsus elongate, more than twice length of article 2. Tarsal articles 1-3 dorsally each with few scattered setae. Tarsal claws pectinate.

Abdomen. Sterna III-VI each with few short setae (in addition to ambulatory setae). Sternum VII of male with apical margin shallowly notched medially, four apical setae.

Male genitalia. Median lobe (Fig. 55 A and B) anopic, apical orifice dorsal, large, apical portion short. Internal sac with broad apical plate.

Female not seen.

Notes. — The range of this genus extends from northern South America to southeastern Mexico. Six species are known, three of which occur in Middle America, and of these one reaches Mexico. Adults are found on logs beneath loose bark, in association with fungi.

Eurycoleus Chaudoir

Eurycoleus Chaudoir, 1848: 124. — Lacordaire, 1854: 129. — Chaudoir, 1869b: 235. — Bates, 1883: 185. — Csiki, 1932: 1381. — Blackwelder, 1944: 58. — Reichardt, 1972: 237-249.

TYPE SPECIES (by monotypy). — *Coptodera fasciatopunctata* Reiche, 1842: 213.

The characteristics presented in the key are sufficient to distinguish members of this genus from other pericalines. The broad flattened body with markedly explanate elytra is reminiscent of members of the New World subgenus *Chelonodema* (genus *Lebia*). However, members of the latter group lack ventral setae from the head, and the penultimate umbilicate puncture of the elytron is displaced inward rather than outward.

Other groups of pericalines exhibiting the explanate body form are found in Africa and Madagascar. They are probably not closely related to *Eurycoleus*.

Description. — Form broad, explanate (Fig. 46), deplanate. Size moderate (standardized body length 7.5-10.0 mm).

Color. Predominantly testaceous, elytra diaphanous, more or less extensively spotted with darker pigment; legs and antennae variously darkened, tergum VII variously darkened.

Microsculpture. Lines on head and pronotum obsolete. Elytra, lines fine, meshes wide, transverse.

Luster. Dorsal surface generally dull. Ventral surface more shining.

Head. Frontal impressions shallow, broad, irregular. Vertex with shallow transverse impression behind eyes, latter large, bulged.

Mouthparts. Mandibles (Fig. 56) very broad, explanate, scrobes obsolescent. Labium (Fig. 57):

mentum edentate, lateral lobes short (M: l/w 0.31), each with apex obliquely truncate, broad; ligula broad apically, quadrisetose. Paraglossae in length subequal to ligula, laterally each with dense covering of short setae; penultimate article of labial palpus anteriorly with one seta near apex, one distinctly preapical.

Prothorax. Pronotum (Fig. 46), maximum width more than 0.66 width of elytra at humeri, weakly convex medially, markedly transverse, broadly explanate laterally; anterior margin shallowly concave; posterior margin truncate medially, sloped obliquely forward laterally; anterior angles very broadly rounded; posterior angles obtuse, sides broadly reflexed, subangulate medially, broad reflexed, not sinuate posteriorly; setae with anterior pair inserted submarginally. Prosternum sparsely setose medially.

Pterothorax. Metasternum sparsely setose medially.

Elytra. Sides broadly rounded, markedly explanate, with thin plate-like extensions; apical margin obliquely truncate, not sinuate; preapical and apical angles rounded. Striae obsolete, surface generally punctate; or striae normally developed, and intervals convex. Umbilical series with penultimate puncture hardly laterad of adjacent punctures.

Legs. Not long and slender, hind tarsus evidently shorter than hind tibia. Middle and hind coxae with ventral surfaces sparsely setose; male front femur without accessory setae; hind tibia with dorsal surface keeled. Hind basitarsus elongate, more than twice length of article 2. Basitarsi sparsely setose. Tarsal claws pectinate.

Abdomen. Sterna III-VII sparsely setose. Sternum VII with apical margin quadrisetose, shallowly notched medially in males, entire in females.

Male genitalia. Median lobe (Fig. 58 A and B) anopic, apical orifice dorsal, very large, apical portion very narrow in ventral aspect; internal sac with large apical plate.

Ovipositor. Average for *Pericalina*, stylus flattened, falcate. (Fig. 59).

Notes. — This endemic New World genus includes six species, whose aggregate range extends from northern South America to northeastern Mexico. Reichardt (1972) revised the genus, and Erwin (personal communication) studied the life history of one species of *Eurycoleus*. The larvae of this species feed on endomychids and the adults are mimics of an erotylid species.

"Pericaloids"

This group, including in the Old World genera such as *Nycteis* (and probably the other Madagascan genera whose males have catopic and/or setose median lobes), *Pericalus*, *Lioptera*, and probably many others, is represented in the New World by only a single subgenus of *Coptodera*.

Coptodera Dejean

Coptodera Dejean, 1825: 273. — Lacordaire, 1854: 140. — Bates, 1869: 69, 71. — Chaudoir, 1869b: 163. — Horn, 1881: 156. — Bates, 1883: 180-183. — Leng, 1920: 66. — Csiki, 1932: 1370. — Darlington, 1934: 116. — Blackwelder, 1944: 57. — Jeannel, 1948: 924, 926. — Ball, 1960: 158. — Habu, 1967: 81. — Darlington, 1968: 110-118. — 1971: 194. — Reichardt, 1972: 238. TYPE SPECIES. — *Coptodera emarginata* Dejean, 1825. (subsequent designation, Blanchard, 1842, plate 20).

Subgenus *Coptodera* (*sensu stricto*)

In addition to the characteristics presented in the key, the following features aid in recognition: labrum almost as long as wide, sharply notched medially; male with middle tibia notched ventrally, near apex; elytra not markedly explanate; male median lobe anopic.

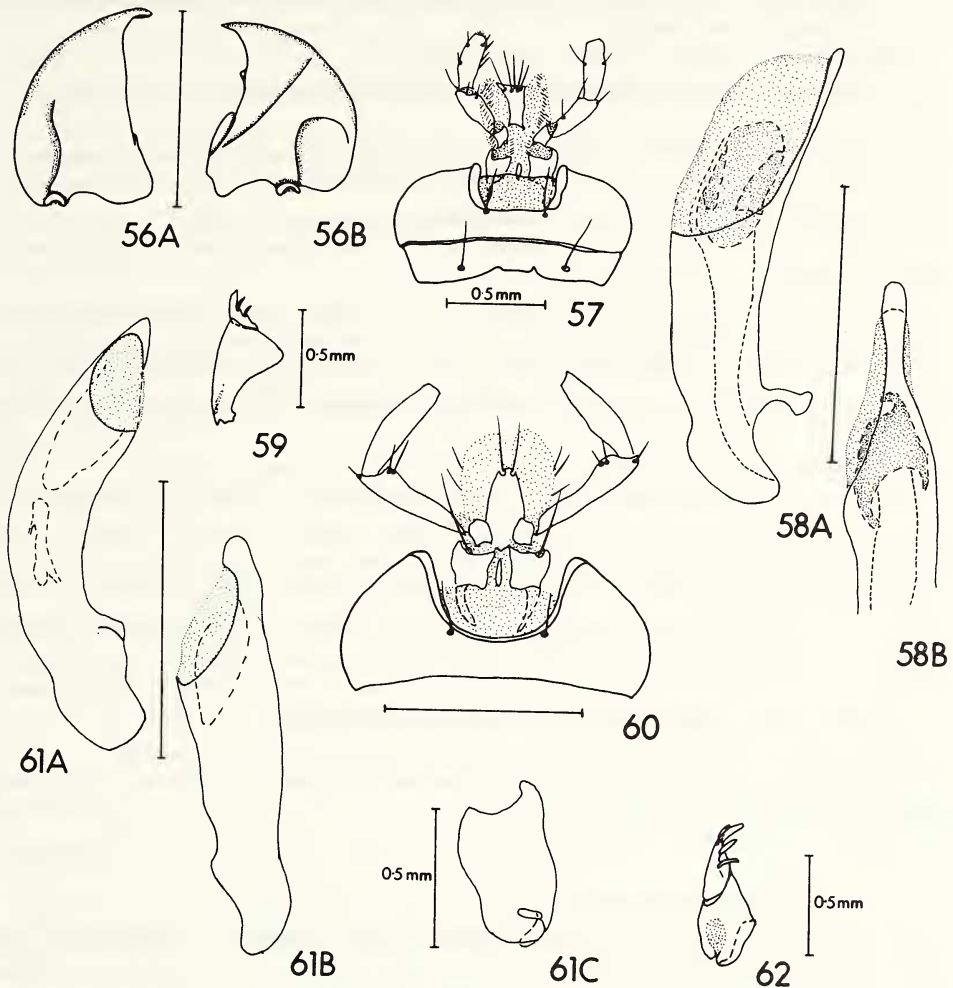


Fig. 56-59. *Eurycoleus macularis* Chaudoir. Fig. 56. Mandibles, dorsal aspect: A, left; B, right. Fig. 57. Labium, ventral aspect. Fig. 58. Male genitalia, median lobe: A, left lateral aspect; B, ventral aspect. Fig. 59. Ovipositor: coxite and stylus. Fig. 60-62. *Coptodera elongata* Chaudoir. Fig. 60. Labium, ventral aspect. Fig. 61. Male genitalia: A, median lobe, left lateral aspect; B, median lobe, ventral aspect; C, left paramere. Fig. 62. Ovipositor: coxite and stylus.

Males of the Old World members of *Coptodera* (subgenus *Coptoderina* Jeannel) have the median lobe catoplic.

Very similar to the members of *Coptodera* are those of *Stenoglossa* and *Lelis*, but they lack setae from the palpiger, and males do not have the middle tibiae notched.

Description. — Form narrow, elongate, somewhat flattened, as in Fig. 47. Size various, small to moderate (standardized body length 4.5-11.0 mm).

Color. Dorsal surface piceous or metallic, elytra dark, concolorous, or variegated with pale markings, or predominantly pale and variegated with dark markings. Ventral surface, antennae, palpi and legs flavous to piceous or black.

Microsculpture. Head, dorsum, lines obsolete, or meshes isodiametric, lines fine. Pronotum, meshes isodiametric to transverse or absent. Elytra, meshes transverse, short, several in row between adjacent pairs of striae.

Luster. Generally shining, faintly iridescent or not.

Head. Frontal impressions obsolete or distinct, smooth or rugulose. Eyes very large and bulged.

Mouthparts. Labrum nearly as long as wide, apical margin sharply and deeply notched. Labium (Fig. 60): mentum not toothed, lateral lobes long (M: l/w 0.42), each lobe pointed apically. Ligula narrow, bisetose; paraglossae longer than ligula, attached to one another toward base, each broadly rounded apically, and with few long setae laterally; palpiger with single seta ventrally.

Prothorax. Pronotum, width more than 0.66 width of elytra at humeri; form various, more or less transverse; apical margin more or less concave, basal margin truncate or sub-lobate, laterally sloped forward; sides reflexed, sinuate or evenly rounded, margins not beaded; two pairs setigerous punctures, insertion of anterior pair submarginal. Prosternum glabrous or very sparsely setose.

Pterothorax. Pterosterna glabrous or very sparsely setose, setae very short.

Elytra. Various in shape, sides rounded to almost parallel, humeri broadly rounded, apical margin more or less sinuate, preapical and apical angles rounded or toothed. Striae 1-8 shallow. Intervals flat. Penultimate umbilical puncture clearly laterad of adjacent punctures.

Legs. Average for Carabidae, not especially long and slender, hind tarsus shorter than hind tibia. Front femur of male without extra setae ventrally. Tibiae with dorsal surfaces more or less keeled, not longitudinally canaliculate. Middle tibia of male with one to three notches apically on ventral surface. Hind basitarsus less than twice length of article 2. Tarsus dorsally with articles sparsely setose throughout. Tarsal claws pectinate.

Abdomen. Sterna glabrous or sparsely setose. Sternum VII with four apical setae.

Male genitalia. As in Fig. 61 A, B, anopic, apical orifice inclined on left side, left paramere broad, irregular in shape, as in Fig. 61 C.

Ovipositor. Stylus (Fig. 62) subcylindrical, more elongate than usual for *Pericalina*, with three or four spines.

Notes. — This tropicopolitan genus ranges to Queensland, in Australia, and northward to the Japanese Archipelago in the Palearctic Region. In the New World, the range of *Coptodera* extends from northern South America to southern United States, and the West Indies. Of the 38 described New World species, 13 occur in Middle America, only, with one occurring both in South America and southern Central America. Members of the genus rest by day beneath loose-fitting bark of dead or dying trees; at night, they are found on the outer side of bark and course along the logs.

CLASSIFICATION OF *PHLOEOXENA* CHAUDOIR

Included here is a taxonomic treatment of the species of *Phloeoxena*. A brief diagnosis of the genus is presented in the preceding section.

Phloeoxena Chaudoir

Coptodera Dejean (in part), 1825: 275.

Phloeoxena Chaudoir, 1869a: 145. — Horn, 1881: 156. — Bates, 1883: 176. — Leng, 1920:

66. — Csiki, 1932: 1359. — Blackwelder, 1944: 57. — Ball, 1960: 159. TYPE SPECIES (here designated). — *Phloeoxena picta* Chaudoir, 1869a: 145.

Description. — Form rather broad, agonoid in subgenus *Oenaphelox* (Fig. 17). Size moderate to small (standardized body length 4.0-9.5 mm).

Color. Body generally piceous, pronotum and elytra concolorous or bicolored, with either flavous or piceous color predominant; elytral markings vermiculate or blotched; head dark.

Microsculpture. Head, dorsum, meshes isodiametric. Pronotum, meshes isodiametric laterally, transverse medially; pteropleura, meshes isodiametric. Elytra, meshes isodiametric, or longitudinal, elevated in form of keeled scales (Fig. 63, 85, 102, 104 and 114), in rows parallel to long axis.

Luster. Dorsum of head, lateral areas of pronotum, and elytra, opaque; central portions of pronotum more or less shining; ventral surface shining to iridescent.

Head. Eyes, average or smaller and flatter than average (Fig. 16-19).

Mouthparts. Generally, as described for subtribe. Labium (Fig. 67 and 99): mentum toothed, lateral lobes long, and each pointed or narrowly rounded at apex (M: l/w 0.41-0.43); ligula broad apically, quadrisetose; paraglossae subequal in length to ligula, asetose.

Prothorax. Pronotum as in Fig. 16-19, 71, 72, 79-81, 95, 97, 100, 105 and 106, width more than 0.66 width of elytral humeri; deplanate medially, transverse; anterior margin shallowly concave, basal margin approximately truncate; lateral margins more or less sinuate or evenly rounded; anterior angles narrowly to moderately broadly rounded, moderately prominent; posterior angles obtuse or rectangular; sides reflexed, not beaded; surface faintly strigulose, median longitudinal impression shallow; shallow linear impression each side, mediad of lateral groove, extended about half length of pronotum from broad, shallow posterior lateral impressions; setae inserted on lateral margins. Prosternum sparsely setose or glabrous.

Pterothorax. Metepisternum longer than wide, or as long as wide. Metasternum subequal to or longer than middle coxal cavity, sparsely setose.

Elytra (Fig. 16-19). Humeri broad; sides rounded, slightly explanate, slightly reflexed; apical margins markedly sinuate, apical angle subacute, preapical angle broadly rounded. Striae shallow or absent, intervals flat, or feebly convex. Interval 3 with two to nine discal setigerous punctures. Umbilical series broadly interrupted medially or not, with 23 or fewer setigerous punctures.

Hind wings. Normal, evidently functional, or small stubs.

Legs. Long, slender, hind tarsus subequal in length to hind tibia. Anterior femur of male with patch of short setae ventrally, near base, or glabrous. Dorsal surface of middle and hind tibia rounded, smooth. Hind basitarsus not elongate, less than twice length of article 2. Tarsal articles dorsally each with single pair of setae apically, or generally but sparsely setose. Tarsal claws with pectinations extended beyond middle of claws.

Abdomen. Sternum VII with apical setae two in males, four in females.

Male genitalia. As in Fig. 68, 73-78, 96, 98, 101 and 107-110; anopic, apical orifice small or moderate in size, inclined on left side; apical portion triangular, small. Internal sac with or without spines.

Ovipositor. Average for Pericalina (Fig. 69 A-E).

Ecological characteristics. — Members of this genus live in tropical or warm temperate forests, at lower elevations on trunks or branches of living or dead trees, usually on or near the surface, beneath small flakes of bark or in moss. At higher elevations, in cloud forest, adults of some species are found on the ground, beneath dead tree branches, or under bark of very rotten logs.

Geographical distribution. — The range of this genus extends throughout Middle America from Panama northward to North Carolina (on the Coastal Plain), in eastern United States; and includes the Greater Antilles of the West Indies (Fig. 113).

Classification. — Chaudoir (1869a) included in three groups the species of *Phloeoxena* known to him: "*species verae*" (four New World species); "*Phloeoxenae Africanae spuriae*" (one species

from Mauritius, off the coast of Africa); and “*Phloeoxenae spuriae*” (three New World species). Alluaud (1933: 15) made the single African species, *Thyreopterus subappendiculatus* Dejean, 1831, type of a new genus, *Mascarenhia*, (see Jeannel, 1949: 931-932 for a figure and description). I have not seen specimens of this species, but am prepared to believe it is not closely related to the New World species included in *Phloeoxena*. For the latter, I agree with Chaudoir that the species known to him should be arrayed in two groups, but with *P. undata* Chaudoir placed among the “*Phloeoxenae spuriae*” rather than with the “*verae*” group. Each of these groups is here classified as a subgenus (the “spurious” one being named *Oenaphelox*), and a third subgenus (*Tacana*) is added for *P. herculeano*, new species.

The basis for including these forms within a single genus, is that, first, the intra-group variation pattern compels one to believe that all of these species are descendents of a single species, and thus they comprise a monophyletic group; and second, this complex is about as divergent from the other New World genera of Pericalina as the latter are from one another. Admittedly, the apotypic character states of *P. herculeano* increase markedly the internal divergence of the genus, and on this basis, one could make a case for placing this species in a genus of its own. However, such a genus would be monobasic, and when possible, I think it best to avoid employing genera having only minimal diversity.

I am prepared to accept monobasic groups at a lower taxonomic level, and so place *P. herculeano* in a group of its own, and rank it at the same level as each of the other two groups of *Phloeoxena*, i.e. at the subgeneric level. I think it useful in moderately diverse genera to employ several ranks in classifying the species, the highest being that of subgenus, followed by group, and if required, sub-group. The species of *Phloeoxena* seem sufficiently divergent to require at least two infrageneric levels to indicate the pattern of relationships.

Each of the three subgenera is definable on phenetic grounds. On phylogenetic grounds, *Tacana* has a number of apotypic character states, which satisfy this requirement for valid taxa. The subgenus *Oenaphelox* is clearly defined by the apotypic character state of spines on the internal sac of the male median lobe, and it, too is a phylogenetically acceptable group. In contrast, the subgenus *Phloeoxena (sensu stricto)*, characterized mainly by absence of synapotypic character states, is unsatisfactory phylogenetically because the group thus defined might not be monophyletic. However, it can be defined polythetically, and is at least a reasonably distinct phenetic group. For the present, I think it best to treat this complex as a subgenus. I also feel confident that eventually evidence will be found to show that this subgenus is indeed monophyletic.

In summary, the 16 known species of *Phloeoxena* are included in three subgenera, defined on the basis of a combination of phenetic and phylogenetic considerations.

Key to the Species of the Genus *Phloeoxena* Chaudoir

1	Elytra bicolored	2
1'	Elytra concolorous	14
2 (1)	Elytra with single large red spot in posterior half	3
2'	Elytra bifasciate or with irregular pattern (Fig. 16, 111, 115)	4
3 (2)	Elytron with two discal setigerous punctures . . . (<i>P.</i>) <i>imitatrix</i> Darlington, p. 189	
3'	Elytron with three discal setigerous punctures . . . (<i>P.</i>) <i>plagiata</i> Darlington, p. 188	
4 (2')	Elytron with blotched pattern (Fig. 111), pronotum entirely flavous, or flavous with dark central spot or stripe, or entirely dark	
 (<i>O.</i>) <i>signata</i> Dejean (in part), p. 213	
4'	Elytron with pair of irregular fasciae, medially joined or not (Fig. 16, 115) . . .	5
5 (4')	Elytron with fasciae not extended to suture (Fig. 16)	
 (<i>O.</i>) <i>undata</i> Chaudoir, p. 208	

- 5' Elytron with fasciae extended to suture (Fig. 115) 6
- 6 (5') Elytron with fasciae broadly joined toward suture, elytra together with cruciate pattern (Fig. 115: 1); eyes bulged, very prominent (*P.*) *megalops* Bates. . 7
- 6' Elytron with fasciae not joined toward suture, eyes less bulged, less prominent. . 9
- 7 (6) Elytron subapically with shiny area with microsculpture meshes isodiametric (*P.*) *m. erwinorum*, new subspecies, p. 194
- 7' Elytron without shiny area subapically, microsculpture meshes of elytra in uniform longitudinally oriented rows 8
- 8 (7') Elytron with anterior and posterior fasciae of about equal width, anterior margin of anterior fascia markedly irregular (Fig. 115: 1) (*P.*) *m. megalops* Bates, p. 194
- 8' Anterior fascia much wider than posterior one (Fig. 93), with anterior margin of former a more or less regular oblique line from suture to about point of stria 6 (*P.*) *m. chiriquina* Bates, p. 195
- 9 (6') Metepisternum quadrate, eyes bulged or not 10
- 9' Metepisternum elongate, lateral margin longer than anterior margin; eyes more or less bulged 13
- 10 (9) Elytron with posterior fascia apical, anterior fascia represented by faintly indicated line of three pale marks (Fig. 115: 5); femora pale (*P.*) *p. apicalis*, new subspecies, p. 202
- 10' Elytron with posterior fascia preapical, anterior fascia complete or nearly so, distinct 11
- 11(10') Elytron with apical angle broadly rounded (Fig. 115: 3), shiny area extended basad beyond area subtended by apical angle, with parasutural spot; eyes not bulged, elytra relatively long (Pl/EI = 0.35) (*P.*) *p. batesi*, new subspecies, p. 199
- 11' Elytron with apical angle acute (Fig. 115: 2), without shiny area apically, parasutural spot present or absent; elytra shorter (Pl/EI = 0.36-0.43) 12
- 12(11') Elytral vermiculations broader (Fig. 115: 2), parasutural spot present or not; pronotum bicolored (*P.*) *p. picta* Chaudoir, p. 201
- 12' Elytral vermiculations narrower (Fig. 115: 4), parasutural spot absent; pronotum concolorous (*P.*) *p. franiae*, new subspecies, p. 200
- 13 (9') Elytron without anterior discal setigerous puncture, pronotum each side with pale stripe (*P.*) *limbicollis* Bates, p. 195
- 13' Elytron with anterior discal setigerous puncture; pronotum concolorous, dark (*P.*) *nigricollis*, new species, p. 195
- 14 (1') Elytron with umbilical series not broadly interrupted medially, including more than 18 setigerous punctures; discal setigerous punctures (3) 4-8; standardized body length 8 mm or more (*T.*) *herculeano*, new species, p. 182
- 14' Elytron with umbilical series broadly interrupted medially, with not more than 15 setigerous punctures; discal setigerous punctures two or three; standardized body length less than 6 mm 15
- 15(14') Pronotum without lateral setae; elytron with two discal setae (*P.*) *montana* Darlington, p. 187
- 15' Pronotum with two pairs of lateral setae; elytron with three discal setae 16
- 16(15') Metepisternum quadrate, short, lateral margin no longer than anterior margin. . 17
- 16' Metepisternum elongate, lateral margin distinctly longer than anterior margin. . 18
- 17(16) Pronotum with sides distinctly sinuate posteriorly; specimen from Mexico (*P.*) *p. unicolor* Chaudoir, p. 200
- 17' Pronotum with sides not, or only slightly sinuate; specimen from Cuba (*P.*) *dealata* Darlington, p. 187

- 18(16') Palpi and legs black; sides of pronotum markedly sinuate posteriorly (Fig. 95) (*O.*) *pluto*, new species, p. 206
- 18' Palpi and legs testaceous or latter bicolored, sides of pronotum sinuate or not. . 19
- 19(18') Pronotum all flavous or predominantly flavous with dark median spot or stripe (*O.*) *signata* Dejean (in part), p. 213
- 19' Pronotum dark, same color as elytra 20
- 20(19') Legs bicolored, with apices of femora and bases of tibiae dark, remainder of legs pale; specimen from Mexico. (*O.*) *geniculata* Chaudoir, p. 209
- 20' Legs uniformly pale; specimen from West Indies 21
- 21(20') Elytra with intervals costate, striae broad. (*P.*) *costata* Darlington, p. 184
- 21' Elytra without costae, smooth, or striae and intervals indistinctly indicated . . 22
- 22(21') Elytron with stria 7 indicated posteriorly. (*P.*) *schwarzi* Darlington, p.
- 22' Elytron smooth, no indication of striae; specimen from locality in Puerto Rico (*P.*) *portoricensis* Darlington, p. 191

Subgenus *Tacana*, new subgenus

TYPE SPECIES. — *Phloeoxena* (*Tacana*) *herculeano*, new species (here designated).

In addition to the characteristics presented in the key, members of this group can be readily recognized by their larger than average size (for *Phloeoxena*) and slender pronotum.

Description. — Form (Fig. 18) slender, elongate, platynoid. Data are presented in Table 2 on variation in standardized body length and in the ratios Hw/Pwm, Hw/Pl, P: Aw/Bw, and Pl/El.

Microsculpture. Elytra, meshes isodiametric, elevated as short, blunt spines (Fig. 63).

Head. Eyes smaller and flatter than average for *Pericalina* (Fig. 18). Antenna, article 3 with preapical setae in addition to terminal ring, article 4 setose for more than half its length.

Mouthparts. Labrum as in Fig. 64. Mandibles as in Fig. 65. Maxillae as in Fig. 66. Labium as in Fig. 67.

Prothorax. Pronotum as in Fig. 18, maximum width greater than width of humeri; sides reflexed, narrowly and indistinctly beaded anteriorly; surface transversely strigulose laterally. Prosternum glabrous.

Pterothorax. Metepisternum about as long as wide. Metasternum glabrous, median length subequal to length of middle coxal cavity.

Elytra. Humeri sloped, narrow; sides obliquely rounded, slightly explanate, reflexed; apical margin feebly sinuate, apical angle obtuse, preapical angle broadly rounded. Striae shallow. Intervals weakly convex. Interval 3 with three to nine setigerous punctures. Umbilical series not broadly interrupted, 19 to 23 setigerous punctures.

Hind wings. Small stubs.

Male genitalia. As in Fig. 68 A and B, anopic; apical portion broad; internal sac without spines.

Female ovipositor. As in Fig. 69 A-E.

This subgenus includes the single species *T. herculeano*, here described as new.

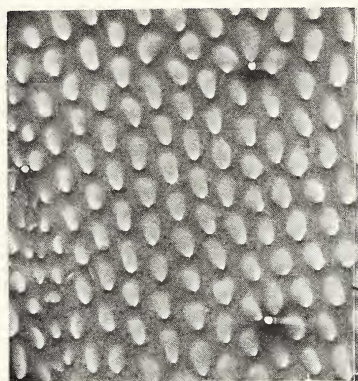
Tacana herculeano new species

Major features of this species are indicated in the key and in the generic description. Details about variation in the following measurements and ratios are presented in Table 2: standardized body length; Hw/Pwm; Hw/Pl; P: Aw/Bw; Pl/El. Males tend to have fewer discal setae than females (modal class for left elytron of males is 5; for females it is 6) but for the number of

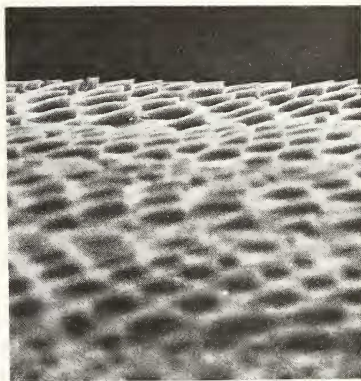
ELYTRAL MICROSCULPTURE OF Phloeoxena herculeano

DORSAL ASPECT

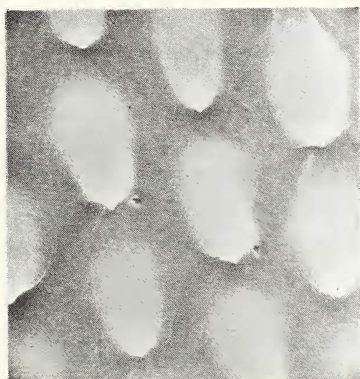
LATERAL ASPECT



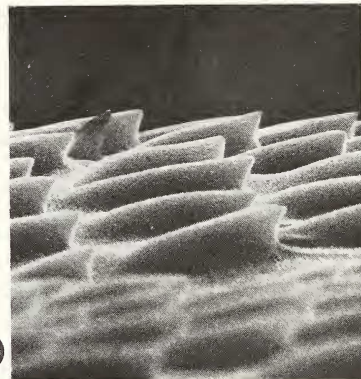
A

20 μ 

B



C

5 μ 

D

63

Fig. 63. *Phloeoxena (Tacana) herculeano* new species. Stereoscan photographs of elytral microsculpture.

umbilical punctures, the order is reverse (modal class for left elytron of males is 21, and for females it is 20).

Type material. — Male holotype and female allotype, labelled: MEX. Chiapas, Volcan Tacaná, s.e. slope, 7800', cloud forest, moss on trees, VII.23.72; MEX. 1972, G. E. Ball, collector. Paratypes, nine males and five females labelled like the holotype; three males and one female labelled: MEX. Chiapas, Sumidero San Antonio (Tacaná), 9000-10000', in a cloud forest, July 24, 1972; and one male and one female labelled MEXICO, Chiapas, 33.7 mi. n. Huixtla, II.26-27. 1966, in bromeliads; G. E. Ball and D. R. Whitehead.

A female, not included in the type series, labelled as follows: GUATEMALA, Dpto. Huehuetenango, Cuchumatanes Mts., Rte 9N, 3 mi. NE San Mateo Ixtatan, 2430 m, VIII.9.74 (D. R. Whitehead, H. F. Frania, G. E. Ball) [UASM].

Table 2. Data on Variation in Selected Measurements and Ratios within a Population Sample of *Phloeoxena (Tacana) herculeano*, New Species, from El Volcan Tacaná, Chiapas, at 7800 Feet above Sea Level.

Character	Males N = 10		Females N = 6	
	Range	Mean	Range	Mean
SBL (mm)	8.5 - 9.3	8.8	8.2 - 9.2	8.7
Hw/Pwm	0.69 - 0.78	0.74	0.74 - 0.81	0.77
Hw/Pl	0.73 - 0.86	0.80	0.78 - 0.82	0.81
P: Aw/Bw	0.93 - 1.14	1.05	1.00 - 1.16	1.04
Pl/EI	0.36 - 0.42	0.40	0.37 - 0.42	0.39

Disposition of type material. — The holotype and allotype are in the USNM. Paratypes are in the following collections: BMNH, California Academy of Sciences, Canadian National Collection, Ottawa, Canada; Instituto Politecnico Nacional de México, México, D. F., MCZ, MNHP, UASM, J. Nègre, Versailles, France, and J. Mateu, Paris, France.

Derivation of the name. — The generic name comes from that of the mountain on which the holotype was collected: El Volcan Tacaná, in southeastern Chiapas. The specific epithet, a noun in apposition, is the Christian name of Sr. Herculeano Morales, who guided me on a number of walks on Tacaná.

Notes on habitat. — These specimens were collected in cloud forests. Most were in moss on the trunks of standing trees, and were found by scraping the moss on to a beating cloth. A few were on the ground, under logs or under loose bark on dead logs. Some of the specimens collected on Tacaná at the beginning of the rainy season (late July) are teneral, suggesting that the onset of the rains marks the period of adult emergence.

Subgenus *Phloeoxena (sensu stricto)*

Characteristics are: color uniform piceous, or elytra bicolored; microsculpture of elytra with meshes flat, or longitudinally oriented, elevated as keeled, vertical scales (Fig. 85, 114); internal sac of male genitalia without spines.

Classification. — This subgenus includes 11 species arranged in two species groups: the *schwarzi* group, of seven West Indian species; and the *picta* group, of four Middle American species.

The *schwarzi* Group

This group is characterized by a combination of: dorsum concolorous, or elytra with single median red spot; microsculpture of elytra keeled or not; scales elongate, keels low or high, linearly arranged (rarely) or not; inhabiting the islands of the West Indies.

Phloeoxena (sensu stricto) costata Darlington

Phloeoxena costata Darlington, 1937: 135. TYPE LOCALITY: Cuba, Oriente Province, Sierra Maestra, Sierra de Cobre.

Comparisons. — The single specimen seen is among the smallest of West Indian *Phloeoxena*, but it has a comparatively wide head.

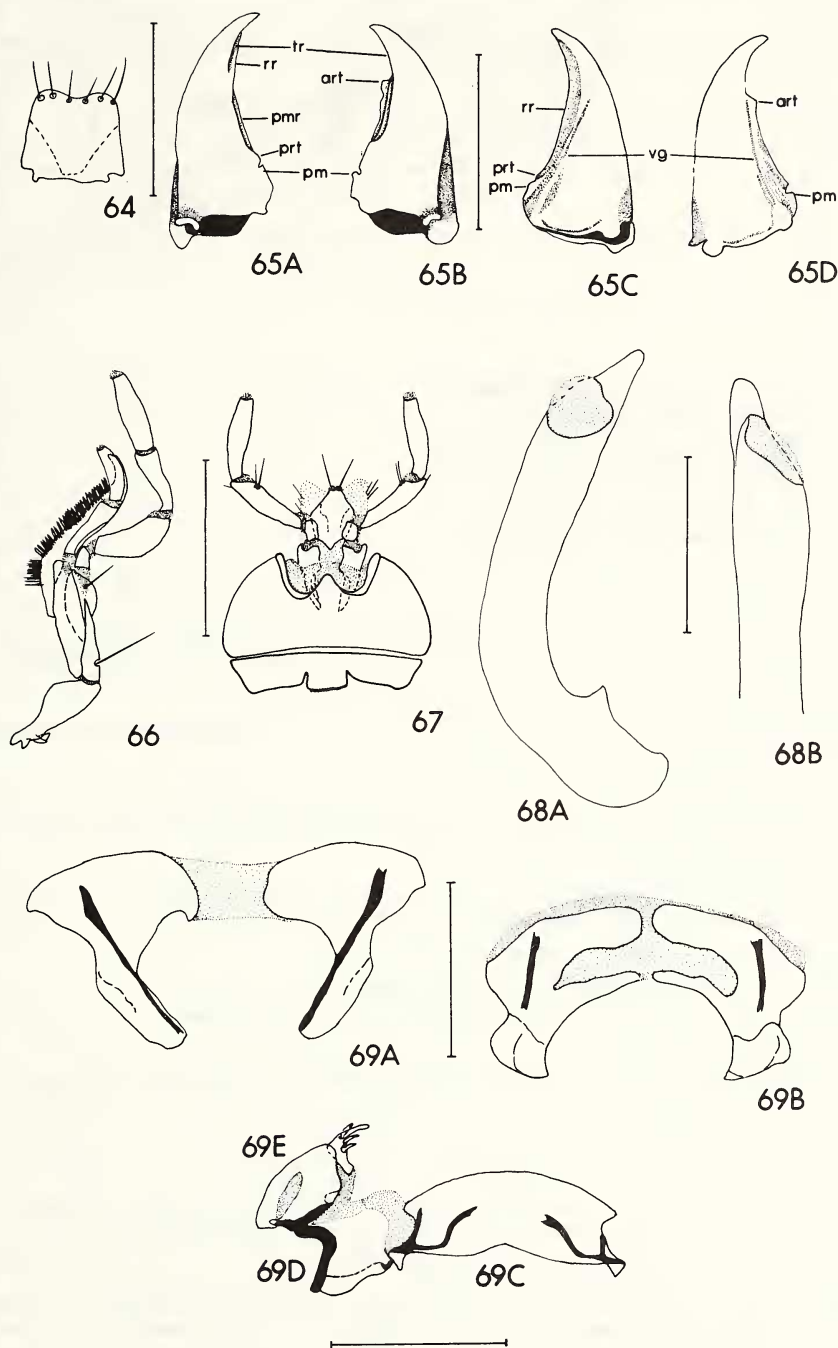


Fig. 64-69. *Phloeoxena (Tacana) herculeano*, new species. Fig. 64. Labrum. Fig. 65. Mandibles: A, left, dorsal aspect; B, right, dorsal aspect; C, left, ventral aspect; D, right, ventral aspect; art - anterior retinacular tooth; pm - premolar tooth; prt - posterior retinacular tooth; rr - retinacular ridge; tr - terebral tooth; tt - terebral tooth; vg - ventral groove. Fig. 66. Maxilla: left, ventral aspect. Fig. 67. Labium, ventral aspect. Fig. 68. Male genitalia, median lobe: A, left lateral aspect; B, dorsal aspect. Fig. 69. Ovipositor and associated sclerites: A, tergum VIII; B, sternum VIII; C, tergum X; D, valvifer; E, coxite and stylus.

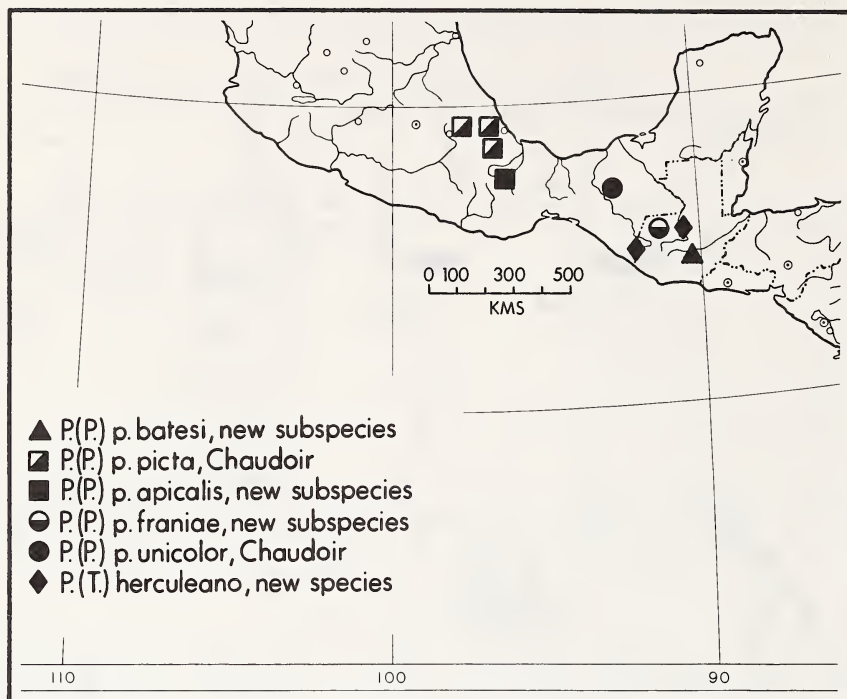


Fig. 70. Map, showing the geographical distribution of *Phloeoxena (Tacana) herculeano* new species, and the subspecies of *P. (sensu stricto) picta* Chaudoir.

Descriptive notes. — Tables 3 to 7 present data on variation in standardized body length and in ratios Hw/Pwm, Hw/Pl, P: Aw/Bw, and Pl/El.

Microsculpture. Head, dorsum with lines coarse, meshes isodiametric, flat. Pronotum, disc with meshes approximately transverse, flat; postero-laterally, with meshes isodiametric, beaded. Elytra, with meshes elongate, scale-like, flat (Fig. 114).

Luster. Dorsal surface generally uniformly shining.

Elytra. Clearly costate, with striae complete and unusually broad.

Male genitalia. Not seen.

Geographical distribution. — This species is known only from the Sierra Maestre Mountains of eastern Cuba (Fig. 114).

Material examined. — One female paratype, collected at Loma del Gato, 3000 feet above sea level, July 3-7, 1936.

Geographical affinities. — As indicated in Fig. 114, this species is in the same general area and mountain system as are representatives of three other species of the *schwarzi* group. However, it is not known to be sympatric with any of them.

Relationships. — The relatively primitive pattern of elytral microsculpture plus seemingly generalized body proportions suggest that this species may be the most plesiotypic member of the genus in the West Indies, and may be as well a plesiotypic survivor of the stem species of the *schwarzi* group.

Phloeoxena (sensu stricto) dealata Darlington

Phloeoxena dealata Darlington, 1937: 136. TYPE LOCALITY: Cuba, Oriente Province, Sierra Maestre Pico Turquino.

Comparisons. — In general, the members of this species are relatively small in size (Table 3), with slightly reduced elytral humeri and primitive microsculpture of the elytra. The reduced wings and microsculpture pattern are shared with *P. montana*, but in form and size specimens of these two species differ markedly from one another.

Descriptive notes. — Tables 3 to 7 present data on variation in standardized body length and in ratios Hw/Pwm, Hw/Pl, P: Aw/Bw, and Pl/El.

Microsculpture. Head and pronotum, as in *P. costata*. Elytra, meshes narrower, low-keeled (Fig. 114).

Luster. As in *P. costata*.

Elytra. Shallowly, narrowly striate, intervals flat and broad.

Male genitalia. Median lobe in left lateral aspect as in Fig. 73 and 74. Apical portion of median lobe longer and narrower than in specimens of other species of the *schwarzi* group. Two specimens were dissected.

For a more detailed description, see Darlington (1937: 136).

Geographical distribution. — This species is known only from the type locality, in Cuba (Fig. 114). Specimens have been collected on Pico Turquino from 3000 to 6000 feet above sea level, mostly at night, in forest, on trunks and branches of fallen trees.

Material examined. — Seven males and seven females, from the type locality.

Geographical affinities. — This species is known only from an isolated peak of the Sierra Maestre Mountains. The ranges of three other members of the *schwarzi* group are farther east in this mountain range (Fig. 114).

Relationships. — The rather broad low-keeled meshes of the elytral microsculpture are the same as in *P. montana*, and I believe that these two are sister species. Their common stock is more plesiotypic than the remaining species of the *schwarzi* group, but more apotypic than *P. costata* (Fig. 118).

Phloeoxena (sensu stricto) montana Darlington

Phloeoxena montana Darlington, 1935: 208. TYPE LOCALITY: Haiti, Mt. La Hotte.

Comparisons. — The members of this species are characterized by the markedly narrow elytral humeri, markedly narrow pronotal base, and by the tarsal claws, each with only three pectines.

Descriptive notes. — Tables 3 to 7 present data on variation in standardized body length and in ratios Hw/Pwm, Hw/Pl, P: Aw/Bw, and Pl/El.

Microsculpture. As described for *P. dealata*.

Luster. Dorsum of head and disc of pronotum shining; postero-lateral areas of pronotum and elytra slightly duller.

Pronotum. As in Fig. 71, lateral margins asetose.

Elytra. Shallowly, narrowly striate, intervals flat and broad.

Male genitalia. Median lobe in left lateral aspect as in Fig. 75. Apical portion more elongate and curved than in other males of the *schwarzi* group. One specimen was dissected.

For a more extensive description, see Darlington (1935: 208).

Geographical distribution. — This species is known only from Mt. La Hotte, in extreme southwestern Haiti. Specimens were collected in leaf mold, moss and rotting wood, in damp forest.

Material examined. — Two males, three females, paratypes.

Geographical affinities. — Another species occurring on Mt. La Hotte is *P. schwarzi*. According to information in the original description, the specimens of *P. montana* were collected near the summit of the mountain, and probably not below 7000 feet altitude. The *P. schwarzi* specimens were collected from 4000 to 5000 feet altitude. Thus, the two species are probably sympatric.

Relationships. — Although markedly different from *P. dealata*, that species and *P. montana* are synapotypic for elytral microsculpture, and I think they are sister species.

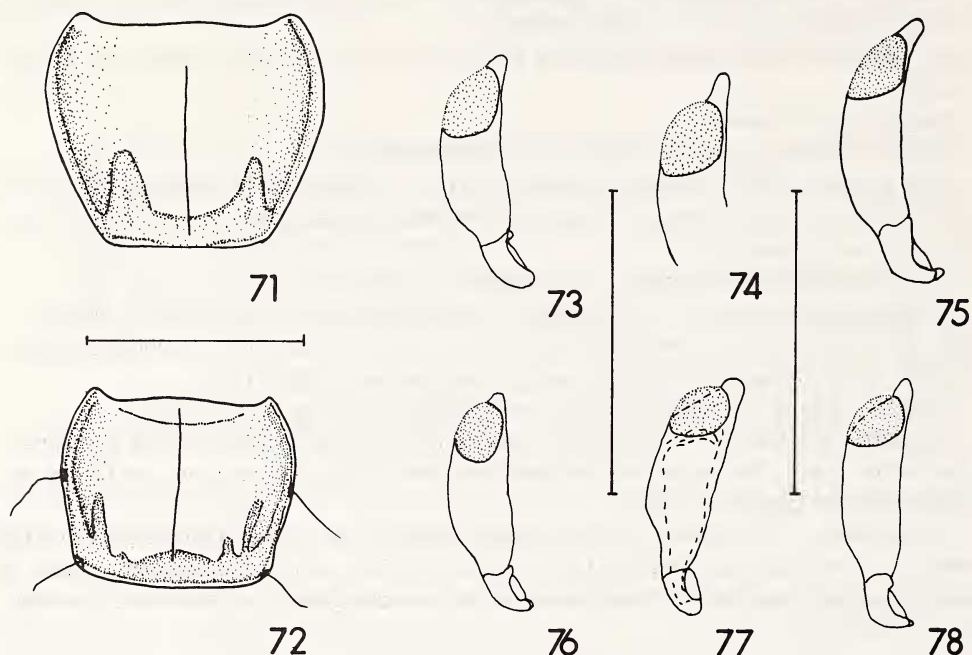


Fig. 71. *Phloeoxena montana* Darlington. Pronotum, dorsal aspect. Fig. 72. *Phloeoxena schwarzi* Darlington. Pronotum, dorsal aspect. Fig. 73-78. Male genitalia, left lateral aspect. Fig. 73 and 74. *Phloeoxena dealata* Darlington. Fig. 75. *Phloeoxena montana* Darlington. Fig. 76. *Phloeoxena imitatrix* Darlington. Fig. 77. *Phloeoxena schwarzi* Darlington. Fig. 78. *Phloeoxena portoricensis* Darlington.

Phloeoxena (sensu stricto) plagiata Darlington

Phloeoxena plagiata Darlington, 1934: 114. TYPE LOCALITY: Cuba, Guantanamo.

Comparisons. — The large, reddish preapical spot on the elytra plus the otherwise almost black color of the dorsal surface distinguish members of this species from all others except *P. imitatrix*. Specimens of the latter lack elytral striae and have longer, more slender pronota.

Descriptive notes. — Tables 3 to 7 present data on variation in standardized body length and in ratios Hw/Pwm, Hw/Pl, P: Aw/Bw, and Pl/El.

Microsculpture. Meshes narrowed to relatively short keeled scales, each scale rather broad, not in contact with its neighbors, and moderately high (Fig. 114).

Luster. Head and disc of pronotum shining; postero-lateral areas of pronotum and dorsal surface of elytra dull.

Elytra. Shallowly, narrowly striate, intervals flat and broad.

Male genitalia. Not examined. Apex of abdomen of holotype damaged and genitalia missing. For a more extensive description, see Darlington (1934: 114).

Geographical distribution. — This species is known only from the type locality (Fig. 114).

Material examined. — Holotype, male (AMNH).

Geographical affinities. — This species is known only from the eastern end of Cuba, near (but not in) the Sierra Maestre Mountains. Three other species of the *schwarzi* group are found in this area, also, but at different elevations, and in different locations.

Relationships. — The closest relative of this species is probably *P. imitatrix*: the two species share an apotypic color pattern and the same type of microsculpture. Probably their common ancestor gave rise to the *schwarzi-portoricensis* stock (Fig. 118).

Phloeoxena (sensu stricto) imitatrix Darlington

Phloeoxena imitatrix Darlington, 1934: 114. TYPE LOCALITY: Cuba, Cayamas, Santa Clara.

Comparisons. — Members of this species are distinguished from all other members of the genus by a combination of dark dorsal coloration with a large red preapical spot on the elytra, smooth elytra without vestiges of striae, and slender elongate pronotum.

Descriptive notes. — Tables 3 to 7 present data on variation in standardized body length and in ratios Hw/Pwm, Hw/Pl, P: Aw/Bw, and Pl/El.

Microsculpture. Generally, as described for *P. schwarzi*, but meshes of elytra as described for *P. plagiata* (Fig. 114).

Luster and elytra. As described for *P. plagiata*.

Male genitalia. Median lobe in left lateral aspect as in Fig. 76. Apical portion short, moderately broad.

For a more extensive description, see Darlington (1934: 114).

Geographical distribution. — This species is known only from Santa Clara and Oriente Provinces, Cuba.

Material examined. — Male, Oriente Province, Gran Piedra Range, 2000-3000 feet above sea level (MCZ); female, paratype, collected at the type locality.

Geographical affinities. — Specimens of other species of the *schwarzi* group have been collected at or near the localities at which specimens of *P. imitatrix* have been collected. Possibly this species and *P. schwarzi* are sympatric at Cayamas (Fig. 114).

Phloeoxena (sensu stricto) schwarzi Darlington

Phloeoxena schwarzi Darlington, 1934: 115. TYPE LOCALITY: Cuba, Cayamas, Santa Clara.

Comparisons. — This species seems to be the most non-descript of West Indian *Phloeoxena*. From those with keeled microsculpture meshes, this species is distinguished by a combination of concolorous dorsum, elytron with only apical portion of stria 7 distinct, and head of average proportions. Superficially, members of this species look like those of *P. dealata*. The latter, however, are appreciably smaller (see Table 3), with microsculpture keels less elevated and not arranged in rows (Fig. 114).

Descriptive notes. — Tables 3 to 7 present data on variation in standardized body length and in ratios Hw/Pwm, Hw/Pl, P: Aw/Bw, and Pl/El.

Microsculpture. Head, dorsum with coarse lines, meshes isodiametric, large, flat. Pronotum, disc with flat transverse meshes, fine lines; postero-lateral areas with isodiametric beaded meshes, lines fine. Elytra, meshes elongate, relatively short, high keels, aligned in longitudinally oriented rows (Fig. 114).

Luster. Head, dorsum and disc of pronotum shining; pronotum with postero-lateral areas

dull; dorsum of elytra dull.

Pronotum. As in Fig. 72.

Male genitalia. Median lobe, left lateral aspect, as in Fig. 77. Apical portion short, very broad. One specimen examined.

For a more extensive description, see Darlington (1934: 115).

Geographical distribution. — This species is known from Cuba and Haiti, the only member of the *schwarzi* group to be so widely distributed (Fig. 114).

Material examined. — Nine males, six females, from the following localities. CUBA. Cayamas (paratypes — MCZ and USNM). HAITI. Roche Croix; Mount La Hotte. DOMINICAN REPUBLIC. Mount Diego de Ocampo (MCZ).

Geographical affinities. — This species may be sympatric with *P. imitatrix* in Cuba, and is parapatric with *P. montana* in Haiti (Fig. 114).

Relationships. — This species and *P. portoricensis* are probably sister species, based on their overall similarities and particularly the reduced elytral striation (partial in *P. schwarzi*, complete in *P. portoricensis*) and vicariant distribution. Of these two species, *P. schwarzi* has the more plesiotypic character states (Table 22 and Fig. 118).

Phloeoxena (sensu stricto) portoricensis Darlington

Phloeoxena portoricensis Darlington, 1939: 99. TYPE LOCALITY: El Yunque, Luquillo Mountains, Puerto Rico.

Comparisons. — The broad heads and smooth elytra of *P. portoricensis* specimens distinguish them readily from the generally similar specimens of *P. schwarzi*. The only other *schwarzi* group specimens with smooth elytra are those of *P. imitatrix*, which however, have bicolored elytra.

Descriptive notes. — Tables 3 to 7 present data on variation in standardized body length and in ratios Hw/Pwm, Hw/Pl, P: Aw/Bw, and Pl/El.

Microsculpture and luster. Generally, as described for *P. schwarzi*, but elytral microsculpture with longer narrower keeled scales (Fig. 114).

Elytra. Smooth, without striae.

Male genitalia. Median lobe, left lateral aspect as in Fig. 78. Apical portion short and moderately wide, as in *P. imitatrix*. One specimen dissected.

For a more extensive description, see Darlington (1939: 99).

Geographical distribution. — This species is known only from Puerto Rico; in the east, from the type locality; and from the west, in the Maricao Forest. The specimens were collected at an elevation of 3000 feet above sea level, under loose bark during the day, and running on trunks of dead trees at night.

Material examined. — Five males, three females, from the type locality (MCZ).

Relationships. — This species is probably the apotypic sister species of *P. schwarzi*. For details, see above.

The *picta* Group

This group is characterized by a combination of: dorsum bicolored, pale markings of elytra fasciate, or dorsum concolorous (Fig. 115); microsculpture of elytra of high keeled, linearly arranged scales, in part or entirely (Fig. 85); inhabiting Middle America from Panama to southeastern Mexico.

Table 3. Data on Variation in Standardized Body Length (mm) among Samples of the *P. schwarzi* Species Group, Subgenus *Phloeoxena*.

Species Name	Locality	N	Range Males	Mean	N	Range Females	Mean
<i>P. costata</i>	CUBA ¹				1	3.20	
<i>P. dealata</i>	CUBA ²	7	2.82 - 3.58	3.35	7	3.08 - 3.60	3.38
<i>P. montana</i>	HAITI ³	2	3.95 - 4.00	3.98	3	3.38 - 3.92	3.70
<i>P. plagiata</i>	CUBA ⁴	1	4.00				
<i>P. imitatrix</i>	CUBA ⁵	1	3.90		1	3.95	
<i>P. schwarzi</i>	CUBA ⁵	1	4.35		1	4.12	
	HAITI:						
	Roche Croix	5	3.72 - 3.98	3.82			
	Mt. La Hotte	1	3.98		3	3.70 - 3.98	3.80
	Mt.D.Ocampo	2	4.12 - 4.32	4.22			
<i>P. portoricensis</i>	PUERTO RICO ⁶	5	3.40 - 4.00	3.71	3	3.40 - 4.10	3.75

1. Sierra de Cobre, Oriente Prov. 2. Pico Turquino. 3. Mt. La Hotte. 4. Guantnamo. 5. Cayamas.
6. El Yunque.

Table 4. Data on Variation in Values for the Ratio Hw/Pwm Among Samples of the *P. schwarzi* Species Group, Subgenus *Phloeoxena*.

Species Name	Locality ¹	N	Range Males	Mean	N	Range Females	Mean
<i>P. costata</i>	CUBA				1	0.85	
<i>P. dealata</i>	CUBA	7	0.72 - 0.80	0.77	6	0.74 - 0.81	0.79
<i>P. montana</i>	HAITI	2	0.82 - 0.83	0.825	3	0.84 - 0.87	0.86
<i>P. plagiata</i>	CUBA	1	0.80				
<i>P. imitatrix</i>	CUBA	1	0.82		1	0.86	
<i>P. schwarzi</i>	CUBA	1	0.84		1	0.84	
	HAITI:						
	Roche Croix	5	0.80 - 0.86	0.82			
	Mt. La Hotte	1	0.76		3	0.83 - 0.87	0.85
	Mt.D.Ocampo	2	0.79	0.79			
<i>P. portoricensis</i>	PUERTO RICO	5	0.84 - 0.90	0.87	3	0.87 - 0.92	0.89

1. See footnotes on Table 3 for additional locality data.

Table 5. Data on Variation in Values for the Ratio Hw/Pl Among Samples of the *P. schwarzi* Species Group, Subgenus *Phloeoxena*.

Species Name	Locality ¹	N	Range Males	Mean	N	Range Females	Mean
<i>P. costata</i>	CUBA				1	1.12	
<i>P. dealata</i>	CUBA	7	0.97 - 1.03	1.00	6	1.00 - 1.03	1.01
<i>P. montana</i>	HAITI	2	0.95 - 0.97	0.96	3	1.00 - 1.09	1.05
<i>P. plagiata</i>	CUBA	1	1.09				
<i>P. imitatrix</i>	CUBA	1	1.00		1	1.09	
<i>P. schwarzi</i>	CUBA	1	1.08		1	1.15	
	HAITI:						
	Roche Croix	5	0.97 - 1.06	1.02			
	Mt. La Hotte	1	1.03		3	1.06	1.06
	Mt.D.Ocampo	2	1.00 - 1.06	1.03			
<i>P. portoricensis</i>	PUERTO RICO	5	1.09 - 1.13	1.11	3	1.16 - 1.21	1.18

1. See footnotes on Table 3 for additional locality data.

Table 6. Data on Variation in Values for the Ratio P: Aw/Bw Among Samples of the *P. schwarzi* Species Group, Subgenus *Phloeoxena*.

Species Name	Locality ¹	N	Range Males	Mean	N	Range Females	Mean
<i>P. costata</i>	CUBA				1	0.93	
<i>P. dealata</i>	CUBA	7	0.91 - 1.00	0.94	7	0.88 - 1.00	0.93
<i>P. montana</i>	HAITI	2	1.13 - 1.21	1.17	3	1.24 - 1.39	1.33
<i>P. plagiata</i>	CUBA	1	0.89				
<i>P. imitatrix</i>	CUBA	1	0.94		1	0.94	
<i>P. schwarzi</i>	CUBA	1	0.90		1	1.00	
	HAITI:						
	Roche Croix	5	0.91 - 0.94	0.93			
	Mt. La Hotte	1	0.92		3	0.91 - 0.97	0.93
	Mt.D.Ocampo	2	0.92	0.92			
<i>P. portoricensis</i>	PUERTO RICO	5	0.94 - 1.06	1.00	3	1.03 - 1.04	1.033

1. See footnotes on Table 3 for additional locality data.

Table 7. Data on Variation in Values for the Ratio Pl/EI Among Samples of the *P. schwarzi* Species Group, Subgenus *Phloeoxena*.

Species Name	Locality ¹	N	Range Males	Mean	N	Range Females	Mean
<i>P. costata</i>	CUBA				1	0.30	
<i>P. dealata</i>	CUBA	7	0.32 - 0.35	0.33	7	0.33 - 0.35	0.34
<i>P. montana</i>	HAITI	2	0.37 - 0.38	0.375	3	0.35 - 0.36	0.353
<i>P. plagiata</i>	CUBA	1	0.31				
<i>P. imitatrix</i>	CUBA	1	0.35		1	0.33	
<i>P. schwarzi</i>	CUBA	1	0.33		1	0.34	
	HAITI:						
	Roche Croix	5	0.32 - 0.34	0.33			
	Mt. La Hotte	1	0.33		3	0.31 - 0.32	0.316
	Mt.D.Ocampo	2	0.29 - 0.31	0.30			
<i>P. portoricensis</i>	PUERTO RICO	5	0.32 - 0.33	0.326	3	0.30 - 0.31	0.306

1. See Footnotes on Table 3 for additional locality data.

Phloeoxena (sensu stricto) megalops Bates

This name is used for three geographically widely separated groups of specimens suspected to be conspecific, but differing sufficiently from one another to suggest that they are taxonomically distinct. Hence, they are treated as subspecies.

The cruciate pale mark on the elytra, relatively large eyes and moderately developed apical portion of the median lobe distinguish members of this species from other members of *Phloeoxena*.

Description. — Tables 8 to 12 present data on variation in standardized body length and in ratios Hw/Pw, Hw/Pl, P: Aw/Bw and Pl/EI.

Color. Following black or piceous: ventral surface, head and pronotum, prothoracic epipleura and portions of elytra as indicated in Fig. 93 and 115:1. Following flavous: elytral epipleura, vermiculate markings of elytra (as in Fig. 93 and 115:1) joined medially in form of cross, legs and antennae. Palpi infuscated or flavous.

Microsculpture. Head and lateral areas of pronotum with meshes isodiametric, beaded, pronotum medially with meshes transverse, wide, beaded. Elytra with meshes costate, long, arranged in parallel longitudinal rows, or each elytron posteriorly with patches of isodiametric microsculpture, meshes flat (Fig. 85 A-D).

Luster. Generally slightly shining, elytra either uniformly silky or with shiny areas postero-medially.

Head. Average for subgenus, eyes more prominent than usual (indicated by relatively high values for ratio Hw/Pl).

Thorax. Pronotum as in Fig. 79, more strongly sinuate than in other fasciate species of subgenus. Metathorax normal, metepisternum with lateral margin clearly longer than anterior margin.

Elytra. Humeri not strongly sloped, preapical margin markedly sinuate, apical angles acute. Disc with 3 setigerous punctures per elytron.

Hind wings. Fully developed.

Male genitalia. Median lobe as in Fig. 82 A and B, apical portion longer than in *P. nigricollis*, but shorter than in *P. limbicollis*.

Geographical distribution. — The range of this species extends from northwestern Guatemala to Panama (Fig. 86).

Phloeoxena megalops megalops Bates

Phloeoxena megalops Bates, 1883: 177, plate 7, Fig. 12. HOLOTYPE male, labelled: "Type H.T. [circular label, ringed with red]; Cerro Zunil 4-5000 ft. Champion, BCA Col 1. 1

Phloeoxena megalops, Bates; *Phloeoxena megalops* Bates [handwritten]". (BMNH). TYPE LOCALITY. Cerro Zunil, Departamento Quezaltenango, Guatemala.

Comparisons. — The predominantly dark, uniformly microsculptured elytra and pale palpi distinguish members of this subspecies from those of the other subspecies of *Phloeoxena megalops*.

Geographical distribution. — Known from the type locality, only.

Material examined. — Two exx., Cerro Zunil, GUATEMALA (BMNH and MNHP).

Phloeoxena megalops erwinorum, new subspecies

Comparisons. — The combination of infuscated palpi and predominantly dark color of elytra, the latter each with a preapical shiny spot, distinguish members of this subspecies from other members of *P. megalops*.

Description. — Tables 8 to 12 present data on variation in mensural characteristics.

Color. Palpi infuscated. Pattern of elytra as in Fig. 115:1. Otherwise, as described for species.

Microsculpture and luster. As described for species, except each elytron with shiny area of isodiametric flat meshes.

Elytra. As described for species, except surface sharply depressed posterior to shiny area.

Type material. — HOLOTYPE male and ALLOTYPE female labelled: COSTA RICA, Puntearenas, 1.5 km NE Monteverde, along antenna road, 10°19'N, 84°44'W, 1500-1700 mts., 10 June 1973; beneath loose bark-stump; No. 49, Notebook No. 2; T. L. and L. J. Erwin; Erwin and Hevel Central American Expedition; ADP 00795 (holotype) and ADP 00796 (allotype) (USNM). Additional PARATYPES seven, six collected by the Erwins on the Erwin-Hevel Central American Expedition, state of Puntearenas, Costa Rica, data in Notebook No. 2: two females, same data as for holotype; male and female, 2.0-3.0 km E. Monteverde, on divide road, 1500-1600 m, 10°18'N, 84°48'W, June 9, 1973, beneath loose bark, male, Monteverde, 10°18'N, 84°49'W, 1390m, June 11, 1973, No. 52, on trees at night; male, Monteverde, road to electric plant, 10°18'N, 84°49'W, 1380m, June 12, 1973, No. 53, beneath loose bark-stump; and male, COSTA RICA, LaPalma, January 1, 1929, under loose bark, F. Nevermann (USNM).

Disposition of type material. — The holotype, allotype and five other paratypes are in the USNM; a male and female paratype are in the UASM.

Derivation of specific epithet. — From the surname of the indefatigable and enthusiastic collectors of most of the type series, my good friends, Terry and LaVerne Erwin.

Geographical distribution. — This subspecies is known from western and central Costa Rica, from an elevation of about 3500 to 6000 feet above sea level (Fig. 86).

Habitat. — According to Dr. Erwin, the beetles were collected in lower montane rain and wet forest and premontane wet forest, under or on the bark of dead trees. They were collected in the company of members of the following carabid genera: *Tachymenis*, *Pachyteles* and *Stenoglossa*.

Phloeoxena megalops chiriquina Bates

Phloeoxena megalops var. *chiriquina* Bates, 1883: 177. HOLOTYPE female, labelled: V de Chiriqui, 2-3000 ft. Champion; BCA Col. 1.1, *Phloeoxena megalops*, Bates; Ph. *megalops* v. *chiriquina* Bates [handwritten]. (BMNH).

Comparisons. — The single known specimen of this subspecies is recognized by a combination of: pale palpi and elytra with a very wide anterior fascia (Fig. 93), without a shiny area posteriorly.

Geographical distribution. — See Fig. 86.

Phloeoxena (sensu stricto) limbicollis Bates, new status

Phloeoxena graphiptera var. *limbicollis* Bates, 1884: 295. HOLOTYPE male, labelled: "Bugaba, Panama Champion; BCA Col 1.1, *Phloeoxena graphiptera*, Chaud; *Phloeoxena graphiptera* v. *limbicollis* [handwritten]. (BMNH). TYPE LOCALITY. Bugaba, Panama.

Comparisons. — Members of this species are readily distinguished from other members of *Phloeoxena* having fasciate elytra by the absence of the anterior pair of discal setae of the elytra. The apical portion of the male median lobe is much broader than in any other species of the subgenus *Phloeoxena* (Fig. 83; cf. Fig. 84).

Description. — Tables 8 to 12 present data on variation in mensural characteristics.

Color. As described for *P. nigricollis*, except pronotum laterally with pale markings extended from base to apex.

Microsculpture and luster. As described for *P. nigricollis*.

Head. Average for subgenus.

Thorax. Pronotum as in Fig. 80 Metathorax of normal size, metepisternum with lateral margin longer than anterior margin.

Elytra. Form as in Fig. 115:2, each elytron with 2 discal setigerous punctures, apical angles acute, sides not strongly rounded.

Hind wings. Fully developed.

Male genitalia. Median lobe as in Fig. 83, apical portion large, apex with keel.

Geographical distribution. — The known range of this species extends from Panama north to Costa Rica. Nothing is recorded, but it probably inhabits lowland tropical forests.

Material examined. — Eleven ex., including the type, from the following localities. COSTA RICA. "Costa Rica" (BCA coll, BMNH); Hamburg Farm, Revantazon, Limon plain, January-November, Nevermann (BMNH and USNM); Chontales (Bates coll., MNHP); Cañas Gordas (BMNH). PANAMA. Type locality only.

Geographical affinities. — The known range of this species overlaps that of *P. megalops*, but these species have not been collected in the same locality.

Relationships. — See discussion of this topic under *P. nigricollis*.

Phloeoxena (sensu stricto) nigricollis, new species

Comparisons. — Members of this species share with those of *P. limbicollis* Bates, *P. p. batesi* new subspecies, *P. p. franiae* new subspecies and *P. p. picta* Chaudoir a similar color pattern of the elytra (cf. Fig. 115: 2, 3 and 4), but each elytron bears three distal setigerous punctures (only two in *P. limbicollis* specimens), and hind wings and metepisternum are fully developed (in members of *P. picta* these structures are reduced).

Description. — Tables 8 to 12 present data on variation in standardized body length and in ratios Hw/Pw, Hw/Pl, P: Aw/Bw and Pl/El.

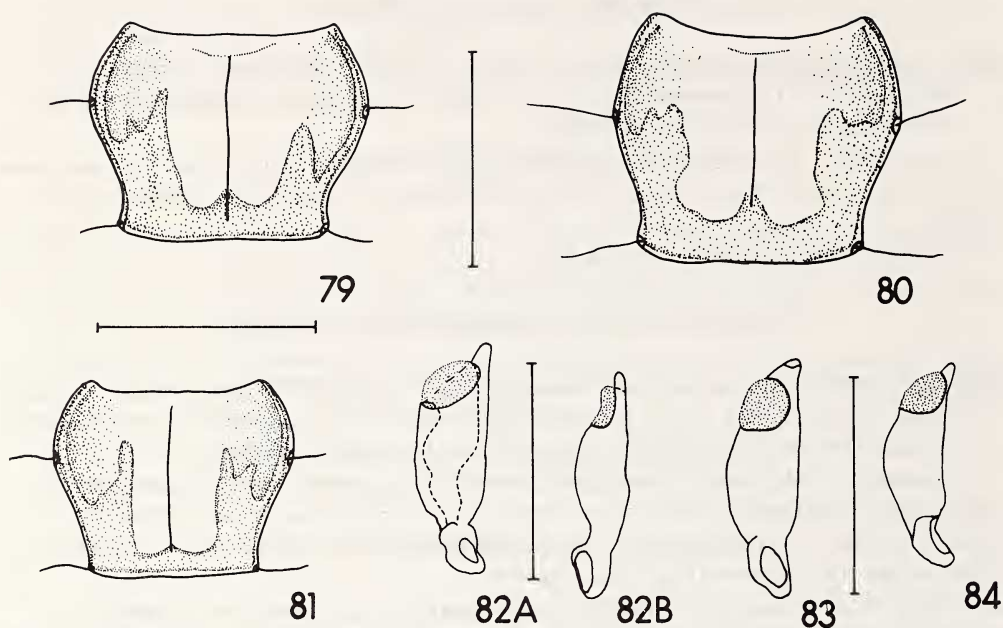


Fig. 79-81. Pronotum, dorsal aspect. Fig. 79. *Phloeoxena megalops megalops* Bates. Fig. 80. *Phloeoxena limbicollis* Bates. Fig. 81. *Phloeoxena nigricollis*, new species. Fig. 82-84. Male genitalia, median lobe. Fig. 82. *Phloeoxena megalops megalops* Bates: A, left lateral aspect; B, ventral aspect, Fig. 83. *Phloeoxena limbicollis* Bates, left lateral aspect. Fig. 84. *Phloeoxena nigricollis*, new species: left lateral aspect.

Color. Following black or piceous: ventral surface, head and pronotum, and portions of elytra as indicated in Fig. 115:2a. Following flavous: pronotal and elytral epipleura, vermiculate markings of elytra (Fig. 115:2a) and appendages.

Microsculpture. Head with meshes isodiametric, beaded. Pronotum with meshes coarse, beaded, disc with meshes isodiametric to transverse, laterally meshes isodiametric. Elytra with meshes keeled, elongate longitudinally (cf. Fig. 85).

Luster. Generally slightly shining, elytra uniformly silky.

Head. Average for genus.

Thorax. Pronotum as in Fig. 81, laterally with two pairs of setae. Metathorax of normal size, metepisternum with lateral margin longer than anterior margin.

Elytra. Humeri moderately rounded; preapical sinuation well developed; apical angles acute; discal setigerous punctures 3 per elytron.

Hind wings. Fully developed.

Male genitalia. Median lobe as in Fig. 84, apical portion short and narrow.

Type material. — HOLOTYPE male, labelled: MEXICO, Chiapas, San Quentin, 16° 24'N, 91° 20'W, 700' above sea level, February 15-20, 1966; D. R. Whitehead and G. E. Ball. PARATYPES 8 all from GUATEMALA, male, 2 females Trece Aguas, Cacao, March 27-29, Schwarz and Baker (USNM); male, Trece Aguas, April 6, E. A. Schwarz (USNM); male, Temahu, Vera Paz, Champion (BMNH); female, San Juan, Vera Paz, Champion (BMNH); female, Chiacaman, Vera Paz, Champion (BMNH).

Disposition of type material. — The holotype is in USNM, and paratypes are in the institutions indicated above.

Derivation of the specific epithet. — Latin, *niger*, black; *collis*, neck; alludes to the uniformly

ELYTRAL MICROSCULPTURE OF Phloeoxena megalops erwinorum

DORSAL ASPECT

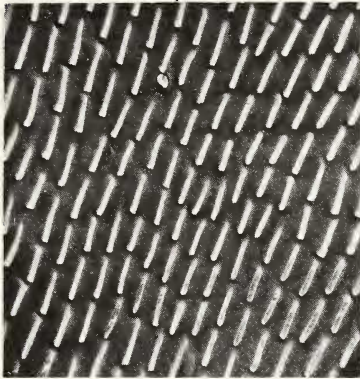
LATERAL ASPECT

10μ

5μ

AREA

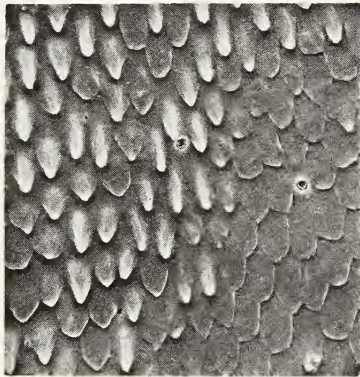
BASAL



A

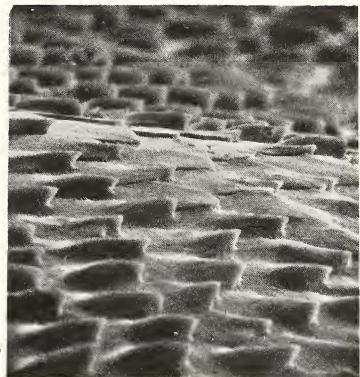


B



C

PRE-APICAL

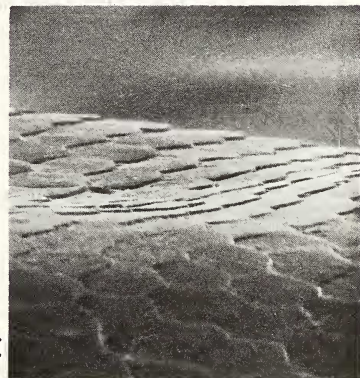


D



E

APICAL



F

Fig. 85. *Phloeoxena (sensu stricto) megalops erwinorum*, new subspecies. Stereoscan photographs of elytral microsculpture.

dark dorsum of the prothorax.

Note on habitat. — The holotype and a female now without a head and not included in the type series, were collected under loose bark of a living tree, in a rain forest.

Geographical distribution. — This species is known only from southern Mexico and Guatemala (Fig. 86).

Geographical affinities. — This low altitude species is allopatric in relation to the other macropterous species of subgenus *Phloeoxena*. The only known locality for the brachypterous *P. p. franiae* is within the range of *P. nigricollis*, but the two are probably parapatric, with the former species living at higher elevations.

Relationships. — Probably this species and *P. limbicollis* are sister species, with the latter having more apotypic character states than the former. These two species probably shared a common ancestry with *P. picta* (Fig. 118).

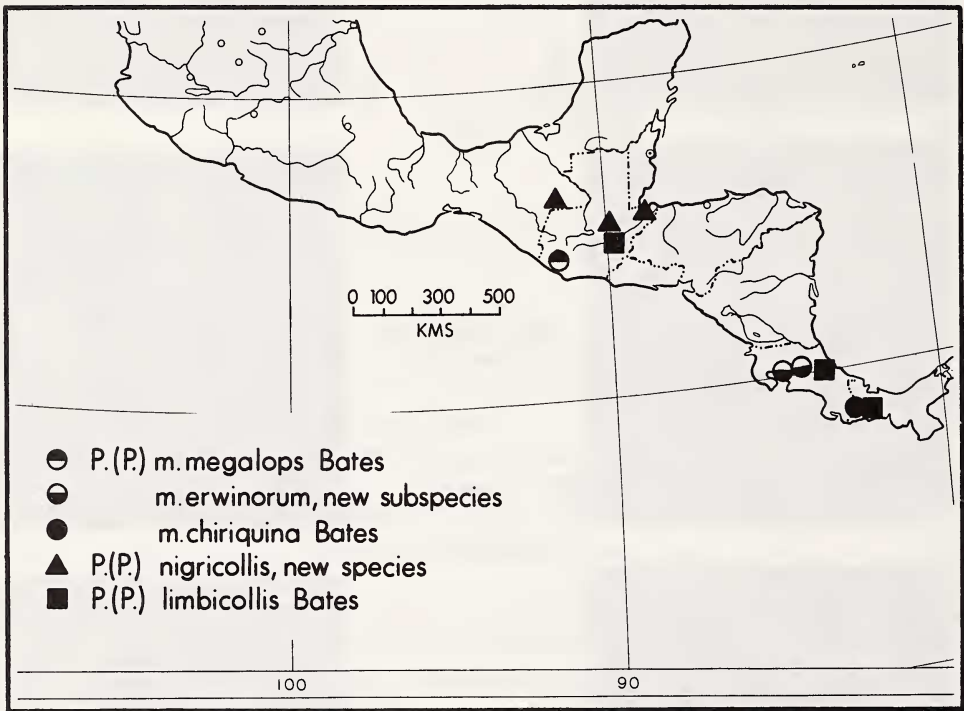


Fig. 86. Map, showing the geographical distribution of the species of the *Phloeoxena (sensu stricto) megalops* complex.

Phloeoxena (sensu stricto) picta Chaudoir

This name is used for five groups of specimens that are probably taxonomically distinct from one another.

The short elytra, bi- or concolorous, with rounded humeri (Fig. 115: 2c-6), and short metepisternum distinguish specimens of this species from the other members of subgenus *Phloeoxena*.

Description. — Tables 8 to 12 present data on variation in standardized body length and in ratios Hw/Pw, Hw/Pl, P: Aw/Bw, and Pl/El.

Color. Following black or piceous: ventral surface, head and pronotum (pale laterally in some individuals), and prothoracic epipleura. Elytra and appendages various. For details, see below and Fig. 94 and 115.

Microsculpture. Elytra with linearly arranged keeled scales, otherwise as described for subgenus.

Luster. Generally slightly shining, elytra uniformly silky.

Head. Average for subgenus, but eyes more or less reduced, (indicated by relatively low values for ratio Hw/Pl).

Thorax. Pronotum as in Fig. 87 to 90. Metathorax reduced, metepisternum with lateral margin subequal in length to anterior margin.

Elytra. Humeri broadly rounded (Fig. 115: 3 to 115: 5), preapical margin sinuate, apical angles acute. Disc with three setigerous punctures per elytron.

Hind wings. Reduced to short stubs.

Male genitalia. Median lobe as in Fig. 91 and 92, apical portion short and more or less broadly rounded, slightly larger than in *P. nigricollis*.

Geographical distribution. — The range of this species extends from northern Guatemala to southeastern Veracruz, Mexico (Fig. 70).

Geographical affinities. — The southern portion of the range of this species is overlapped by the northern portions of the ranges of *P. nigricollis* and *P. megalops*, but *P. picta* is not known to be sympatric with any other species of subgenus *Phloeoxena*.

Relationships. — Some members of this species share same color pattern of the elytra with the more plesiotypic *P. nigricollis* and *P. limbicollis*, and the same form of genitalia with *P. nigricollis*. The absence of hind wings establishes the apotypic position of *P. picta*. I regard this species as the apotypic sister species of the stock that gave rise to *P. nigricollis* and *P. limbicollis*.

Phloeoxena picta batesi, new subspecies

Phloeoxena graphiptera var., Bates, 1883: 177. A female, labelled: "S. Geronimo, Guatemala Champion; BCA Col 1.1, *Phloeoxena graphiptera*, Chaud; *Phloeoxena graphiptera* var. [hand-written]. TYPE LOCALITY. San Geronimo, Guatemala.

Note on type material. — Bates selected this specimen as being distinct at the variety level from specimens of typical *P. graphiptera* (conspecific with *P. picta*), and *P. g.* var. *limbicollis*. Because he did not provide a name for this "variety" which seems to represent a distinct subspecies, one is provided here.

Comparisons. — The single specimen of this subspecies has the same color pattern of elytra as have some members of *P. p. picta*, but has relatively larger eyes and longer elytra.

Description. — See Tables 8 to 12 for mensural data. Elytral color pattern as in Fig. 115:3. Following flavous: ventral surface medially, appendages and elytral epipleura. Microsculpture and luster as described for species except dark preapical area of elytra with meshes more or less isodiametric, flat, surface more shining.

Derivation of subspecific epithet. — From the surname of H. W. Bates, who recognized the distinctness of this specimen, but neglected to name its taxon.

Geographical affinities. — The single locality (Fig. 70) is the southernmost for this species, and is close to the locality of *P. p. franiae*.

Relationships. — Because of its relatively plesiotypic body proportions and color pattern, and its proximity to the ranges of the more plesiotypic *P. nigricollis* and *P. limbicollis*, I regard *P. p. batesi* as closest to the ancestral stock of *P. picta*.

Phloeoxena picta franiae, new subspecies

Comparisons. — Members of this subspecies are similar to those of *P. p. apicalis*, differing in size (smaller, on average), development of elytral markings (in *P. p. franiae* specimens, anterior fascia more complete, posterior fascia narrower), and in color of femora (infuscated in *P. p. franiae*, uniformly pale in *P. p. apicalis*). Specimens of *P. p. franiae* are also similar in elytral pattern to some specimens of *P. p. picta*, but in the latter the fasciae are wider (Fig. 115: 4; cf. Fig. 94).

Description. — See Tables 8 to 12 for mensural data. Elytral color pattern as in Fig. 115: 4. Elytral epipleura and appendages flavous except infuscated basal halves of femora.

Type material. — HOLOTYPE male, labelled: GUATEMALA Dpto. Huehuetenango, Cuchumatanes Mts., 5.6 mi. n. Santa Cruz Barillas, 1280m, VIII.7-8.74; D. R. Whitehead, H. E. Frania, G. E. Ball collectors. PARATYPES (including ALLOTYPE) 2 males, 4 females, labelled same as holotype.

Disposition of type material. — The holotype and allotype are in USNM. A single paratype is in the collections of each of the following institutions: BMNH, IPNM, MNHP, MCZ, UASM, and USNM.

Notes on habitat. — The specimens were collected in tropical montane forest, from moss on standing trees, living or dead. The branches of the higher trees formed an unbroken canopy, and the area beneath was well shaded.

Derivation of the subspecific epithet. — A patronymic, based on the surname of Henry E. Frania, my field assistant, who collected the first specimens.

Geographical affinities. — Probably *P. p. franiae* and *P. nigricollis* are parapatric, with the latter species occurring at lower elevations. The range of *P. p. franiae* is closest to that of *P. p. batesi*, but is in the same general mountain system as is the range of *P. p. unicolor* (Fig. 70).

Relationships. — This subspecies is probably the sister group of *P. p. unicolor*, based on the geographical affinities of the two forms and on their reduced color pattern of the elytra.

Phloeoxena picta unicolor Chaudoir, new combination

Phloeoxena unicolor Chaudoir, 1869a: 148. HOLOTYPE male, in Oberthür Box 126, in front of this box label: unicolor Chaud Mexique A. Deyrolle. Specimen labelled: Mexique [handwritten]; A. Deyrolle [handwritten]; Ex Musaeo Chaudoir [red print]. (MNHP). TYPE LOCALITY. Mexico. - Bates, 1883: 177.

Note on type material. — The data associated with the holotype coincide with the data in the original description.

Comparisons. — The largest known specimens of subgenus *Phloeoxena* are included in this subspecies. The uniformly piceous dorsal surface distinguish members of this subspecies from all others.

The holotype is substantially smaller than the specimens collected in Chiapas, but I did not take exact measurements of the former specimen. It was otherwise identical with the other examples included in this subspecies.

Description. — (details based on two males, collected in Chiapas, Mexico. A third male from which the elytra were removed for stereoscan microscope study of microsculpture was not used for measurements). See Tables 8 to 12 for mensural data. Color generally rufo-piceous to piceous, except rufous antennae and palpi. Eyes flattened, as indicated by low values for ratio Hw/Pl (Table 10). Median lobe of male genitalia as in Fig. 92.

Geographical distribution. — This species is known only from the state of Chiapas, Mexico (Fig. 70).

Notes on habitat. — The specimens were collected in cloud forest, both in litter on the ground and under bark of a fallen tree.

Material examined. — Three males (including the holotype), one female, all from Mexico. CHIAPAS. Rte. 195, 11.5 mi. n. Pueblo Nuevo, 5200'. April 26-27, 1966, Ball and Whitehead, (UASM). Yerba Buena Hospital, 1.5 mi. n. Pueblo Nuevo, 7200'; cloud forest, June 21, 1972, Ball and P. A. Meyer (UASM).

Geographical affinities. — The range of this subspecies is adjacent to that of *P. p. franiae* (see above, and Fig. 70). No other species of subgenus *Phloeoxena* has been collected in the same localities.

Relationships. — The geographical proximity and general structural similarities of this subspecies and *P. p. franiae* are taken as evidence of sister group status for these two.

Phloeoxena picta picta Chaudoir

Phloeoxena picta Chaudoir, 1869a: 145. Type material, 4 exx. in front of this box label: *picta* Chaud Mexique Sallé. LECTOTYPE male (here selected), first specimen, labelled: "Ex Musaeo Chaudoir" [red print] (MNHP). TYPE LOCALITY. Mexico. — Bates, 1883: 176.

Phloeoxena graphiptera Chaudoir, 1869a: 147. Type material, 3 exx. in Oberthür Box 126, in front of this box label; *graphiptera* Chaud, Mexique, Sallé. LECTOTYPE male (second specimen, here selected), labelled: Ex Musaeo Chaudoir [red print] (MNHP). PARATYPES, 2 females, labelled same as lectotype. TYPE LOCALITY. Mexico. — Bates, 1883: 177 (in part). NEW SYNONYMY.

Notes on type material. — Data associated with the specimens of *P. graphiptera* and *P. picta* in the Oberthür collection coincide with information provided in the original descriptions.

Notes on synonymy. — The only difference between the sympatric *P. graphiptera* and *P. picta* is that the elytra of the former specimens have well developed parasutural spots because of the more extensive development of the anterior fasciae (Fig. 115: 2). The parasutural spots are lacking from the elytra of specimens of *P. picta* (Fig. 94). Otherwise, the two groups of specimens are virtually identical and thus, I conclude, are conspecific. Because the two forms are sympatric, I conclude that they are also consubspecific.

Comparisons. — Some members of this subspecies share with those of *P. p. batesi* a vermiculate color pattern complete with parasutural spots. However, the elytra are relatively shorter in *P. p. picta* than in *P. p. batesi* (values for ratio Pl/EI higher in the latter — see Table 12), and the eyes are less prominent in *P. p. picta* (value for ratio Hw/Pwm lower — see Table 9). Members of *P. p. picta* lacking parasutural spots resemble members of *P. p. franiae*, but the vermiculate markings of the latter are narrower and the pronotum is generally all black.

Description. — Elytral pattern as in Fig. 94 and 115: 2. Following flavous: pronotal and elytral epipleura, posterior-lateral areas of pronotum, and appendages. Median lobe of male average for species.

Geographical distribution. — This subspecies is known only from southeastern Mexico, on the lower slopes of Volcan Orizaba in Veracruz (Fig. 70).

Material examined. — Nineteen specimens, including the type series, from the following localities: MEXICO, Veracruz — Cordova, Sallé Coll. (BMNH); Jalapa (BMNH and UAIC); and Las Vigas (BMNH).

Geographical affinities. — This is the northernmost subspecies of *Phloeoxena picta*, and its geographical range is near that of *P. p. apicalis*.

Relationships. — Probably this subspecies and *P. p. apicalis* are sister groups. Both exhibit apotypic color patterns: *P. p. picta*, with a bicolored pronotum; and *P. p. apicalis* with reduced elytral markings.

Phloeoxena picta apicalis, new subspecies

Comparisons. — Members of this subspecies share with those of *P. p. unicolor* predominantly dark elytra and flattened eyes but differ by having some clearly defined pale marks on the elytra (Fig. 115: 5).

Description. — See Tables 8 to 12 for mensural data. Elytra bifasciate, but anterior fascia broken and faint, and posterior one broad, very close to apical margin (Fig. 115: 5). Appendages flavous, body otherwise rufopiceous. Eyes less prominent than average, indicated by low value for ratio Hw/Pl (Table 10).

Type material. — HOLOTYPE female, labelled: MEXICO Oaxaca, 16.9 mi. s. Valle Nacional, 3600', May 4-5, 1966, Ball and Whitehead (USNM). PARATYPE Female, same locality as for holotype, but collected August, 1965 (UASM).

Derivation of specific epithet. — An adjectival form of *apex* (Latin for tip), in allusion to the proximity of the posterior elytral vermiculation to the apex of the elytra.

Note on habitat. — The specimens were collected in a montane cloud forest, in litter near a small depression in the ground that intermittently holds water. By analogy with the habits of *Phloeoxena herculeano*, members of this subspecies probably live both on the ground and in moss on tree trunks.

Geographical affinities. — This is the only taxon of subgenus *Phloeoxena* known from Oaxaca (Fig. 70), and this subspecies and *P. p. picta* are the only taxa of this subgenus known from north of the Isthmus of Tehuantepec.

Relationships. — See discussion of this topic under *P. p. picta*.

Table 8. Data on Variation in Standardized Body Length (SBL) (mm) Among Samples of the *P. picta* Species Group, Subgenus *Phloeoxena*.

Species Name	Locality	N	Range Males	Mean	N	Range Females	Mean
<i>P. m. megalops</i>	Cerro Zunil, Guat.	1	4.08				
<i>P. m. erwinorum</i>	Puentearenas, C.R.	4	4.20 - 4.32	4.28	4	3.16 - 4.28	4.08
	La Palma, C.R.	1	3.88				
<i>P. m. chiriquina</i>	Vol.de. Chiriqui, Pan.				1	3.80	
<i>P. limbicollis</i>	Revantazon, C.R.	4	4.08 - 4.32	4.23	4	3.84 - 4.32	4.08
	Cañas Gordas, C.R.				1	4.56	
	Bugaba, Panama				1	4.32	
<i>P. nigricollis</i>	San Quentin, Mex.	1	3.68				
	Trece Aguas, Guat.	2	3.96 - 4.16	4.03	2	3.32 - 3.48	3.40
	Livingston, Guat.	1	3.24				
	Temahu, Guat.	1	3.96				
	San Juan, Guat.				1	3.88	
	Chiacaman, Guat.				1	3.68	
<i>P. p. batesi</i>	S. Geronimo, Guat.				1	3.60	
<i>P. p. franiae</i>	S.C. Barillas, Guat.	3	3.64 - 4.00	3.80	4	3.60 - 4.20	3.90
<i>P. p. unicolor</i>	Pueblo Nuevo, Mex.	2	5.68 - 5.84	5.76	1	6.44	
<i>P. p. picta</i>	Cordova, Mex.	1	4.08		1	3.80	
	Jalapa, Mex.	2	4.24 - 4.40	4.32	1	4.20	
<i>P. p. apicalis</i>	Valle Nacional, Mex.				2	4.00 - 4.48	4.24

Table 9. Data on Variation in Values for the Ratio Hw/Pwm Among Samples of the *P. picta* Species Group, Subgenus *Phloeoxena*

Species Name	Locality	N	Range Males	Mean	N	Range Females	Mean
<i>P. m. megalops</i>	Cerro Zunil, Guat.	1	0.90				
<i>P. m. erwinorum</i>	Puentearenas, C.R.	4	0.93 - 1.00	0.98	4	0.96 - 1.04	0.99
	La Palma, C.R.	1	0.96				
<i>P. m. chiriquina</i>	Vol. de Chiriqui, Pan.				1	0.92	
<i>P. limbicollis</i>	Revantazon, C.R.	3	0.87 - 0.92	0.90	4	0.88 - 0.92	0.90
	Cañas Gordas, C.R.				1	0.87	
	Bugaba, Pan.				1	0.83	
<i>P. nigricollis</i>	San Quentin, Mex.	1	0.88				
	Trece Aguas, Guat.	2	0.85 - 0.86	0.855	2	0.87 - 0.88	0.875
	Livingston, Guat.	1	0.86				
	Temahu, Guat.	1	0.85				
	San Juan, Guat.				1	0.89	
	Chiacaman, Guat.				1	0.88	
<i>P. p. batesi</i>	San Geronimo, Guat.				1	0.88	
<i>P. p. franiae</i>	S.C. Barillas, Guat.	3	0.79 - 0.88	0.83	4	0.83 - 0.88	0.86
<i>P. p. unicolor</i>	Pueblo Nuevo, Mex.	2	0.82 - 0.84	0.83	1	0.78	
<i>P. p. picta</i>	Cordova, Mex.	1	0.84		1	0.82	
	Jalapa, Mex.	2	0.78 - 0.83	0.80	1	0.79	
<i>P. p. apicalis</i>	Valle Nacional, Mex.				2	0.79 - 0.80	0.795

Table 10. Data on Variation in Values for the Ratio Hw/Pl Among Samples of the *P. picta* Species Group, Subgenus *Phloeoxena*.

Species Name	Locality	N	Range Males	Mean	N	Range Females	Mean
<i>P. m. megalops</i>	Cerro Zunil, Guat.	1	1.24				
<i>P. m. erwinorum</i>	Puentearenas, C.R.	4	1.17 - 1.27	1.23	4	1.24 - 1.33	1.27
	La Palma, C.R.	1	1.25				
<i>P. m. chiriquina</i>	Vol. de Chiriqui, Pan.				1	1.32	
<i>P. limbicollis</i>	Revantazon, C.R.	4	1.09 - 1.14	1.12	4	1.09 - 1.13	1.105
	Cañas Gordas, C.R.				1	1.04	
	Bugaba, Panama				1	1.09	
<i>P. nigricollis</i>	San Quentin, Mex.	1	1.16				
	Trece Aguas, Guat.	2	1.04 - 1.10	1.07	2	1.10 - 1.11	1.105
	Livingston, Guat.	1	1.11				
	Temahu, Guat.	1	1.05				
	San Juan, Guat.				1	1.10	
	Chiacaman, Guat.				1	1.15	
<i>P. p. batesi</i>	S. Geronimo, Guat.				1	1.05	
<i>P. p. franiae</i>	S.C. Barillas, Guat.	3	0.92 - 0.96	0.94	4	0.96 - 1.00	0.99
<i>P. p. unicolor</i>	Pueblo Nuevo, Mex.	2	0.96 - 1.07	1.02	1	1.00	
<i>P. p. picta</i>	Cordova, Mex.	1	1.00		1	1.00	
	Jalapa, Mex.	2	0.93 - 0.97	0.95	1	1.04	
<i>P. p. apicalis</i>	Valle Nacional, Mex.				2	0.93 - 1.04	0.985

Table 11. Data on Variation in Values for the Ratio P: Aw/Bw Among Samples of the *P. picta* Species Group, Subgenus *Phloeoxena*.

Species Name	Locality	N	Range Males	Mean	N	Range Females	Mean
<i>P. m. megalops</i>	Cerro Zunil, Guat.	1	1.05				
<i>P. m. erwinorum</i>	Puentearenas, C.R.	4	1.00 - 1.05	1.025	4	1.00 - 1.10	1.05
	La Palma, C.R.	1	1.05				
<i>P. m. chiriquina</i>	Vol. de Chiriqui, Pan.				1	1.00	
<i>P. limbicollis</i>	Revantazon, C.R.	3	1.00	1.00	4	1.00 - 1.05	1.025
	Cañas Gordas, C.R.				1	1.00	
	Bugaba, Panama				1	1.09	
<i>P. nigricollis</i>	San Quentin, Mex.	1	1.00				
	Trece Aguas, Guat.	2	0.95 - 1.04	1.00	2	1.00	1.00
	Livingston, Guat.	1	1.00				
	Temahu, Guat.	1	0.87				
	San Juan, Guat.				1	1.00	
	Chiacaman, Guat.				1	1.07	
<i>P. p. batesi</i>	S. Geronimo, Guat.				1	1.12	
<i>P. p. franiae</i>	S.C. Barillas, Guat.	3	1.00	1.00	4	1.10 - 1.18	1.12
<i>P. p. unicolor</i>	Pueblo Nuevo, Mex.	2	0.96 - 1.07	1.02	1	1.00	
<i>P. p. picta</i>	Cordova, Mex.	1	1.00		1	1.00	
	Jalapa, Mex.	2	0.87 - 1.00	0.94	1	0.96	
<i>P. p. apicalis</i>	Valle Nacional, Mex.				2	1.09	

Table 12. Data on Variation in Values for the Ratios PI/EI Among Samples of the *P. picta* Species Group, Subgenus *Phloeoxena*.

Species Name	Locality	N	Range Males	Mean	N	Range Females	Mean
<i>P. m. megalops</i>	Cerro Zunil, Guat.	1	0.32				
<i>P. m. erwinorum</i>	Puentearenas, C.R.	4	0.32 - 0.33	0.33	4	0.31 - 0.33	0.32
	La Palma, C.R.	1	0.32				
<i>P. m. chiriquina</i>	Vol. de Chiriqui, Pan.				1	0.31	
<i>P. limbicollis</i>	Revantazon, C.R.	3	0.33 - 0.34	0.34	4	0.33 - 0.34	0.335
	Cañas Gordas, C.R.				1	0.34	
	Bugaba, Panama				1	0.33	
<i>P. nigricollis</i>	San Quentin, Mex.	1	0.32				
	Trece Aguas, Guat.	2	0.33 - 0.34	0.335	2	0.33	0.33
	Livingston, Guat.	1	0.35				
	Temahu, Guat.	1	0.32				
	San Juan, Guat.				1	0.32	
	Chiacaman, Guat.				1	0.32	
<i>P. p. batesi</i>	S. Geronimo, Guat.				1	0.35	
<i>P. p. franiae</i>	S.C. Barillas, Guat.	3	0.39 - 0.43	0.410	4	0.38 - 0.40	0.39
<i>P. p. unicolor</i>	Pueblo Nuevo, Mex.	2	0.36 - 0.39	0.375	1	0.35	
<i>P. p. picta</i>	Cordova, Mex.	1	0.39		1	0.38	
	Jalapa, Mex.	2	0.39 - 0.41	0.40	1	0.38	
<i>P. p. apicalis</i>	Valle Nacional, Mex.				2	0.36 - 0.39	0.375

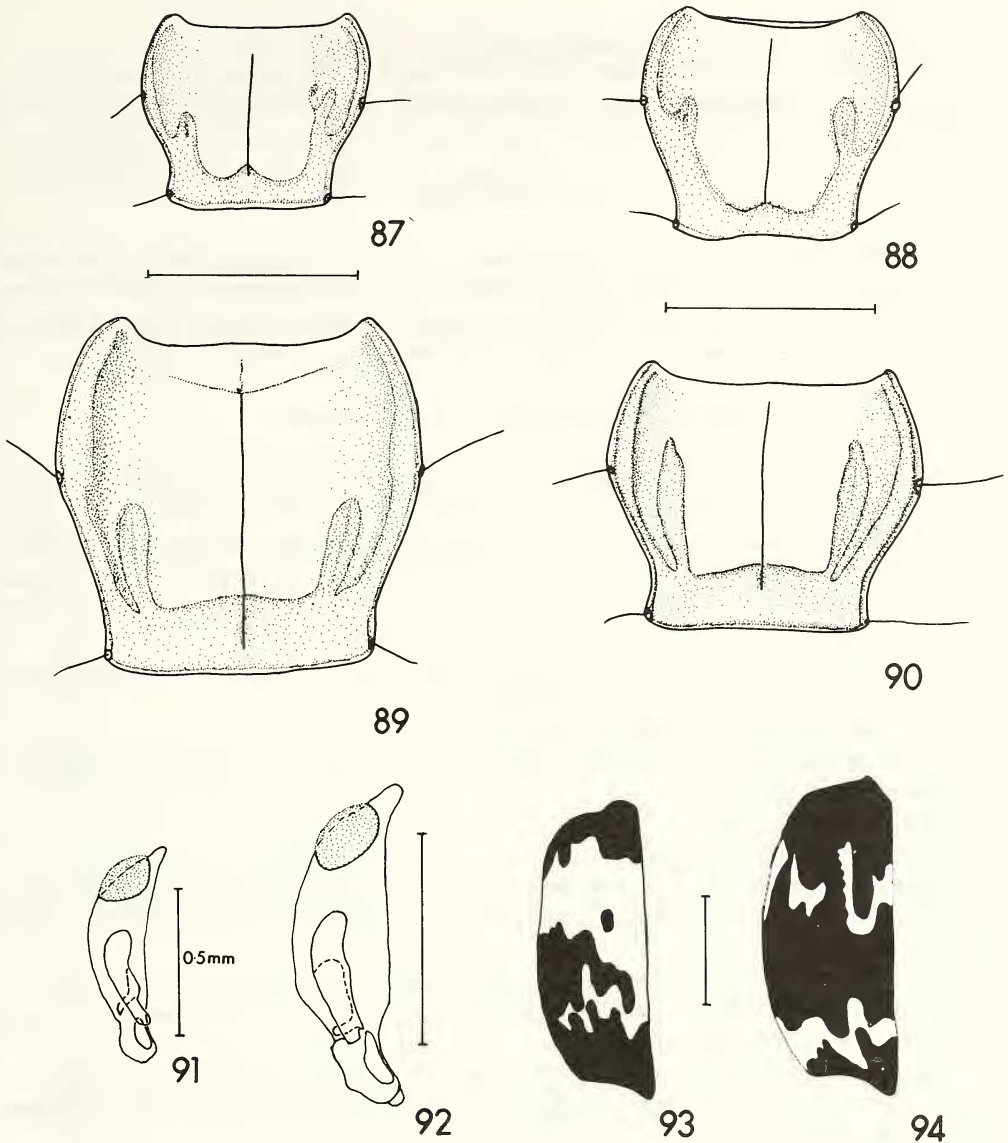


Fig. 87-90. Pronota, dorsal aspect. Fig. 87. *Phloeoxena picta batesi*, new subspecies. Fig. 88. *Phloeoxena picta franiae*, new subspecies. Fig. 89. *Phloeoxena picta unicolor* Chaudoir. Fig. 90. *Phloeoxena picta apicalis*, new subspecies. Fig. 91-92. Male genitalia, median lobe, left lateral aspect. Fig. 91. *Phloeoxena picta franiae*, new subspecies. Fig. 92. *Phloeoxena picta unicolor* Chaudoir. Fig. 93-94. Left elytron, color pattern. Fig. 93. *Phloeoxena megalops chiriquina* Bates. Fig. 94. *Phloeoxena picta picta* Chaudoir.

Subgenus *Oenaphelox*, new subgenus

TYPE SPECIES: *Coptodera signata* Dejean, 1825 (here selected).

Characteristics are: Color of dorsal surface uniform piceous or bicolored piceous and flavous (Fig. 16 and 17); microsculpture of elytra with meshes elongate, scale-like, flat (Fig. 104 A-D) and in contact laterally, or keeled, not in contact laterally (Fig. 102 and 104 E-F); internal sac

of male genitalia with one to nine spines (Fig. 96 A, 98, 101, 107-110).

Classification. — The four included species are arranged in two groups: *pluto* group, with *P. pluto*; and the *signata* group, with *P. undata* Chaudoir, *P. geniculata* Chaudoir, and *P. signata* Dejean.

The *pluto* Group

This group is characterized by a combination of: color black (including palpi and antennae); microsculpture of dorsum more or less isodiametric, meshes flat; pronotum with sides sinuate, hind angles well developed; male genitalia with median lobe short and broad, apical portion in lateral aspect short; internal sac of male genitalia with armature weakly developed.

Phloeoxena (Oenaphelox) pluto, new species

Comparisons. — The completely black color of the body and appendages distinguishes the only known specimen of this species from members of all other species of *Phloeoxena*. Additional features of use in identification are the markedly sinuate sides of the pronotum and internal sac of male genitalia with slightly sclerotized spines. Within the subgenus *Phloeoxena*, the body is relatively wide and short as indicated by values for the ratios Hw/Pwm, and Hw/Pl (Tables 14 and 15).

Description. — Tables 13 to 17 present data on variation in standardized body length and in ratios Hw/Pwm, Hw/Pl, P: Aw/Bw, and Pl/El.

Color. Black, except dark piceous tarsal articles.

Microsculpture. Meshes more or less isodiametric, flat, meshes on head larger than those on pronotum and elytra.

Luster. Dorsum shining.

Head. Eyes prominent, bulged.

Pronotum. As in Fig. 95, transverse; anterior margin moderately incurved; lateral margins markedly sinuate posteriorly; anterior angles prominent, rounded; posterior angles acute; sides broadly reflexed.

Elytra. In form average for subgenus, but apical margins more strongly sinuate in other species of *Oenaphelox*; striae shallow, broad; intervals feebly convex, more convex posteriorly. Punctuation average for subgenus.

Male genitalia. Median lobe as in Fig. 96 A and B, short and broad, with apical portion in lateral aspect short. Internal sac with armature weakly developed: one short, blunt spine, one lightly sclerotized area.

Type material. — Holotype (only known specimen) labelled: Panama Pwa Prov., Cerro Campana, 850 m, 8°40'N, 79°56'W, 29 Mar. 72, Blvin, ADP 33344 (USNM).

Derivation of specific epithet. — From classical mythology, for the god of the Underworld, in allusion to the funereal color of the holotype.

Geographical affinities. — The single locality for this species is possibly within the southern limits of the range of *P. signata*, but is far south of the known range of the other species of subgenus *Oenaphelox* (Fig. 103).

Relationships. — This species is the most distinctive of the subgenus *Oenaphelox*, and is probably the most plesiotypic. Although the prothorax is relatively short and broad, the hind angles are distinct. The microsculpture is plesiotypic, and the median lobe is like that of males of subgenus *Phloeoxena*. The rudimentary armature of the internal sac suggests the beginning of a trend, leading to the more complex armature exhibited by other members of *Oenaphelox*.

The *signata* Group

This group is characterized by a combination of: palpi and antennae pale; dorsum usually bicolored; male genitalia with median lobe slender, elongate, apical portion in lateral aspect well developed, internal sac with several large spines.

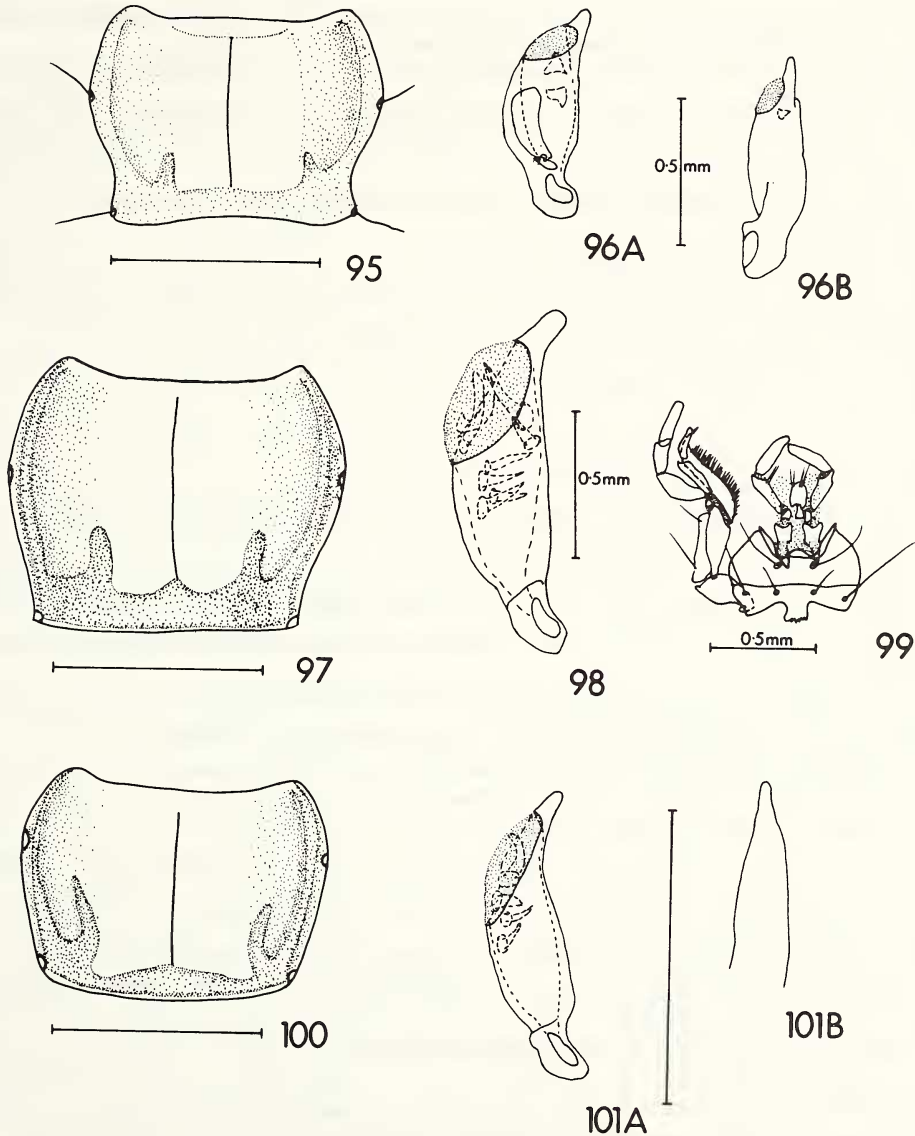


Fig. 95-96. *Phloeoxena (Oenaphelox) pluto*, new species. Fig. 95. Pronotum, dorsal aspect. Fig. 96. Male genitalia, median lobe, and armature of internal sac: A. left lateral aspect; B. ventral aspect. Fig. 97-98. *Phloeoxena (Oenaphelox) undata* Chaudoir. Fig. 97. Pronotum, dorsal aspect. Fig. 98. Male genitalia, median lobe, and armature of internal sac, left lateral aspect. Fig. 99-101. *Phloeoxena (Oenaphelox) geniculata* Chaudoir. Fig. 99. Right maxilla and labium, ventral aspect. Fig. 100. Pronotum, dorsal aspect. Fig. 101. Median lobe and armature of internal sac: A. left lateral aspect; B. ventral aspect.

Phloeoxena (Oenaphelox) undata Chaudoir

Phloeoxena undata Chaudoir, 1869a: 147. HOLOTYPE female, in Oberthür Box 126, labelled: Ex Musaeo Chaudoir [red print], in front of this box label: undulata Chaud Mexique Sallé. (MNHP). TYPE LOCALITY. Mexico. — Bates, 1883: 177.

Note on type material. — The data on the box label coincide only partly with the information in the original description: Sallé is recorded in both, but the specific epithet differs. Nonetheless, the characters of the type specimen agree with the description, and the name *P. undulata* has not been published; thus I have no doubt about the identification.

Comparisons. — In addition to color characteristics, specimens of *P. undata* are distinguished from members of the other species of subgenus *Oenaphelox* by the narrowly reflexed, clearly sinuate sides of the pronotum, and the narrow head relative to width of pronotum (see Table 15). Pale color of legs distinguishes specimens of *P. undata* from those of *P. geniculata*. The apical part of the median lobe of male *P. undata* is relatively broad, compared to that of *P. geniculata*. The spines of the internal sac are of two sizes, large and small, in contrast to the internal sac of *P. signata* males, with all spines large.

Description. — Form as in Fig. 16. Tables 13 to 17 present data on variation in standardized body length, and in ratios Hw/Pwm, Hw/Pl, P:Aw/Bw and Pl/El.

Color. Piceous, except following flavous (pale): palpi, proepipleura, elytral epipleura, lateral margins and two narrow, vermiculate fasciae on elytra. Antennae and legs flavous to lightly infuscated.

Microsculpture. Head and pronotum, dorsally meshes isodiametric. Elytra, meshes beaded anteriorly, flat behind posterior fascia (Fig. 102).

Luster. Dorsum generally dull, except area of elytra behind posterior fascia shining.

Head. Eyes prominent, moderately bulged.

Pronotum. As in Fig. 97; anterior margin moderately deeply concave; lateral margins slightly sinuate posteriorly; anterior angles prominent, rounded; posterior angles rectangular; sides moderately reflexed; disc slightly convex; posterior lateral impressions continuous with lateral grooves.

Elytra. Humeri broadly rounded; sides subparallel, slightly flared; and reflexed posterior margins sinuate-truncate. Striae broad, very feebly indicated; setae average for genus.

Male genitalia. Median lobe as in Fig. 98, curved, apical portion moderately long, apex broad. Internal sac with 9 spines, five large ones toward apex (infolded position), four smaller ones more basad. Two specimens dissected.

Notes on habitat. — Specimens of this species were collected in July and October in cloud forest, from foliage and trunks of standing trees. They were taken with a beating cloth by disturbing piles of dead leaves that had accumulated on networks of vines; or by scaling off loose bark from the trunks of standing trees. In general, I did not note the tree species from which the beetles were taken. However, some were found on *Podocarpus* specimens. My impression is that the beetles were not associated with particular trees, but rather with suitable hiding places. Martin (1958) gives a detailed description of the area.

Geographical relations. — This species seems to be parapatric with *P. signata*. In the Sierra de Guatemala and environs, specimens of *P. undata* were collected at altitudes of about 3800 feet. At the foot of the mountains, near Encino, Tamaulipas, specimens of *P. signata* were collected. Neither species was found at intermediate elevations, but an intensive effort was not made to sample in the latter areas.

Geographical distribution. — This species is known in Mexico from three localities: two specific areas, and one state record. The former two are in the east (Fig. 103), in the Sierra Madre Oriental, and the adjacent portion of the Trans-Volcanic Sierra.

Relationships. — This species is the most distinctive of the *signata* group, and is probably the most plesiotypic. The body proportions are average for the genus, as a whole, and the sides of the pronotum are sinuate, and the hind angles are distinct. Members of this species and those of *P. geniculata* share predominantly dark coloration of the body, and spines of two different sizes in the internal sac of the males, but these are interpreted as plesiotypic similarities. These species, though allopatric, also share a similar distribution pattern: both are known only from middle altitudes, and evidently do not enter lowland tropics. This is probably an apotypic character, but probably not synapotypic.

Material examined. — 31 exx., including the holotype, from the following localities.

MEXICO. "OAXACA" [BMNH]. TAMAULIPAS. Rancho del Cielo, Sierra de Guatemala, 8 mi. n.e. Gomez Farias, 3800', October 6-10, 1965, (Ball and Whitehead), and July 24-29, 1971 (Ball and Ball) [UASM]. VERACRUZ. Cordova [BMNH].

Phloeoxena (Oenaphelox) geniculata Chaudoir

Phloeoxena geniculata Chaudoir, 1869a: 151. LECTOTYPE male (here selected), one of 2 exx., in Oberthür Box 126, labelled "Ex Musaeo Chaudoir" [red print] in front of this box label: *geniculata* Chaud, Mexique, Cuernavaca, Boucard [MNHP]. ALLOTYPE female, similarly labelled, pinned next to male. TYPE LOCALITY. Cuernavaca, Morelos, Mexico. — Bates, 1883: 178.

Note on type material. — Data on the box label coincide with information given in the original description.

Comparisons. — Specimens of this species are mainly dark in color, and the dorsal surface is uniformly dull. The head is relatively wide compared to width of pronotum, and is evidently the result of proportionately larger eyes than those of other species of subgenus *Oenaphelox* (see Table 14). Spines of the internal sac of the male genitalia are of two different sizes (as in males of *P. undata*); this distinguishes males of *P. geniculata* from those of *P. signata*, the latter having uniformly large spines in the internal sac.

Description. — Form as in Fig. 17. Tables 13 to 17 present data on variation in standardized body length and in ratios Hw/Pwm, Hw/Pl, P: Aw/Bw and Pl/El.

Color. Piceous-black, except following constantly infuscated: antennal articles 5-11 and palpi; following constantly flavous: antennal articles 1-4 and elytral epipleura. Legs pale, or infuscated with apices of femora and bases of tibiae pale.

Microsculpture. Dorsum with meshes isodiametric, beaded. Meshes of elytra broad, but keeled (Fig. 104 E, F).

Luster. Dorsum dull.

Head. Eyes markedly prominent.

Pronotum. As in Fig. 97, agonoid, broad; anterior margin moderately deeply concave; lateral margins incurved posteriorly, not sinuate; anterior angles broadly rounded, moderately prominent; posterior angles broadly rounded; sides moderately reflexed, disc slightly convex, posterior-lateral impressions shallow, continuous with broad lateral grooves.

Elytra. Humeri broadly rounded; sides subparallel, slightly reflexed; posterior margins sinuate, sub-truncate. Striae broad, shallow but distinct. Setigerous punctures average for genus.

Male genitalia. Median lobe as in Fig. 101, curved, apical portion narrow, elongate, apex narrow. Internal sac with 4 spines apical one (in inverted position) large, basal 3 smaller. (One specimens dissected).

Geographical variation. — The legs are mainly dark in specimens from the Balsas Basin and Trans-Volcanic Sierra. To the northwest (Nayarit), however, the legs are pale (single female seen).

Notes on habitat. — Specimens of this species have been collected in tropical thorn forests typical of the Balsas drainage growing on a lava field (pedregal), and in open oak woods adjacent to this forest. They have also been collected on the Trans-Volcanic Sierra in badly cut-over areas that probably once supported oak forests.

In the Cuernavaca area (Balsas drainage) the beetles were collected from standing trees, by scaling off loose bark on to a beating cloth. In the localities on the Trans-Volcanic Sierra, the beetles were found under loose bark on logs laying on the ground.

Geographical distribution. — The known altitudinal range of this species is from 4300 to 5700 feet above sea level. The species is known only from Mexico, in the northwest from the western slopes of the Sierra Madre Occidental southward across the Trans-Volcanic Sierra to the Balsas Basin, and thence to the eastern slopes of the Oaxacan highlands.

Geographical affinities. — The ranges of this species and of *P. signata* are parapatric. The two species may be partly sympatric, but they have not been collected from the same locality.

Relationships. — Members of this species share with those of *P. signata* an agonoid type of pronotum, and comparatively large eyes relative to length of pronotum (Table 15), and are probably closely related. However, *P. geniculata* specimens exhibit proportionately larger eyes relative to pronotal width (Table 14), and are probably at the end of a morphocline for eye size. On the other hand, specimens of *P. signata* exhibit a pronotum more broadly reflexed, and the internal sac of the male genitalia has uniformly large spines. Thus, this species is at the end of morphoclines for these two characteristics. The two species are probably sister species; their common ancestor was probably derived from a common ancestry with *P. undata*.

Material examined. — A total of 14 exx., including types, from the following localities in Mexico. GUERRERO. Chilpancingo [BMNH]. JALISCO. nr. El Rincon, 35.7 mi. n.w. Los Volcanes, 5700'. August 11, 1967 (Ball, Erwin and Leech) [UASM]. MICHOACAN. 8.1 mi. e. Villamar, 5500', August 31, 1966, (Ball and Whitehead) [UASM]. MORELOS. Cuernavaca [MNHP]. 3.6 mi. e. Cuernavaca, 4600', pedregal, November 24, 1965 (Ball and Whitehead) [UASM]. 5.4 mi. e. Cuernavaca, 4600', pedregal, June 29-30, 1966 (Ball and Whitehead) [UASM]. Cañon de Lobos, 9.1 mi. e. Cuernavaca, 4300', July 24, 1966 (Ball and Whitehead) [UASM]. NAYARIT. Arroyo Canaveral, near Jesus Maria, July 15, 1955 (B. Malkin) [Univ. Calif. Berkeley]. OAXACA. Yolos (= Yolox) (Sallé) [BMNH].

Table 13. Data on Variation in Standardized Body Length Among Samples of Species of Subgenus *Oenaphelox*.

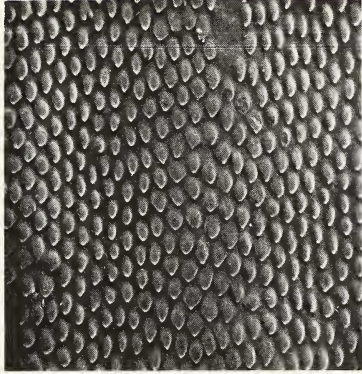
Species Name	Locality	N	Range Males	Mean	N	Range Females	Mean
<i>P. pluto</i>	PANAMA ¹	1	4.36				
<i>P. undata</i>	MEXICO Tamps. ²	15	4.04 - 4.68	4.34	12	3.80 - 4.56	4.20
<i>P. geniculata</i>	MEXICO Morelos ³	1	4.08		5	4.24 - 4.88	4.45
<i>P. signata</i>	U.S.A. Alabama ⁴	8	4.08 - 4.64	4.42			
	U.S.A. Florida ⁵	4	4.12 - 4.56	4.37	4	4.52 - 4.96	4.73
	MEXICO Oaxaca ⁶	1	4.32		2	4.00 - 4.56	4.28
	PANAMA Paraiso	2	3.76 - 4.40	4.08	3	3.92 - 4.32	4.08

1. Cerro Campana 850 m. 2. Rancho del Cielo. 3. east of Cuernavaca. 4. Mobile. 5. Crescent City. 6. vicinity of Juchatengo, 7. Paraiso.

ELYTRAL MICROSCULPTURE OF *Phloeoxena undata*

DORSAL ASPECT

20μ



A

AREA

BASAL

LATERAL ASPECT

5μ



B

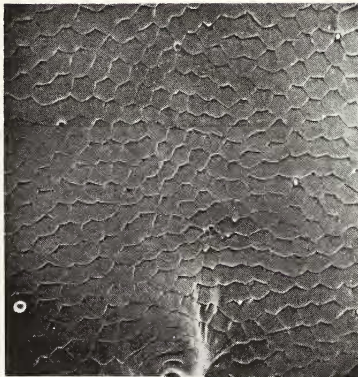


C

PRE - APICAL



D



E

APICAL



F

Fig. 102. *Phloeoxena (Oenaphelox) undata* Chaudoir. Stereoscan photographs of elytral microsculpture.

Table 14. Data on Variation in Values for the Ratio Hw/Pwm Among Samples of Species of Subgenus *Oenaphelox*.

Species Name	Locality ¹	N	Range Males	Mean	N	Range Females	Mean
<i>P. phuto</i>	PANAMA	1	0.92				
<i>P. undata</i>	MEXICO Tamps.	15	0.74 - 0.81	0.78	12	0.68 - 0.83	0.78
<i>P. geniculata</i>	MEXICO Morelos	1	0.87		5	0.82 - 0.94	0.87
<i>P. signata</i>	U.S.A. Alabama	8	0.75 - 0.79	0.77			
	U.S.A. Florida	4	0.72 - 0.78	0.75	4	0.74 - 0.78	0.76
	MEXICO Oaxaca	1	0.78		2	0.80 - 0.81	0.805
	PANAMA Paraiso	2	0.76 - 0.82	0.79	3	0.76 - 0.81	0.79

1. See footnotes on Table 13 for additional locality data.

Table 15. Data on Variation in Values for the Ratio Hw/Pl Among Samples of Species of Subgenus *Oenaphelox*.

Species Name	Locality ¹	N	Range Males	Mean	N	Range Females	Mean
<i>P. phuto</i>	PANAMA	1	1.34				
<i>P. undata</i>	MEXICO Tamps.	15	0.96 - 1.12	1.04	12	1.00 - 1.12	1.07
<i>P. geniculata</i>	MEXICO Morelos	1	1.24		5	1.24 - 1.36	1.30
<i>P. signata</i>	U.S.A. Alabama	8	1.14 - 1.26	1.20			
	U.S.A. Florida	4	1.08 - 1.21	1.16	4	1.16 - 1.22	1.19
	MEXICO Oaxaca	1	1.23		2	1.25 - 1.26	1.255
	PANAMA Paraiso	2	1.22 - 1.28	1.25	3	1.25 - 1.32	1.28

1. See footnotes on Table 13 for additional locality data.

Table 16. Data on Variation in Values for the Ratio P: Aw/Bw Among Samples of Species of Subgenus *Oenaphelox*.

Species Name	Locality ¹	N	Range Males	Mean	N	Range Females	Mean
<i>P. phuto</i>	PANAMA	1	0.92				
<i>P. undata</i>	MEXICO Tamps.	15	0.88 - 0.96	0.92	12	0.88 - 1.04	0.94
<i>P. geniculata</i>	MEXICO Morelos	1	0.84		5	0.75 - 0.96	0.89
<i>P. signata</i>	U.S.A. Alabama	8	0.83 - 0.96	0.89			
	U.S.A. Florida	4	0.92 - 0.93	0.922	4	0.90 - 0.93	0.91
	MEXICO Oaxaca	1	0.92		2	0.89 - 0.92	0.90
	PANAMA Paraiso	2	0.86 - 0.92	0.89	3	0.85 - 0.88	0.86

1. See footnotes on Table 13 for additional locality data.

Table 17. Data on Variation in Values for the Ratio PI/EI Among Samples of Species of Subgenus *Oenaphelox*.

Species Name	Locality ¹	N	Range Males	Mean	N	Range Females	Mean
<i>P. phuto</i>	PANAMA	1	0.29				
<i>P. undata</i>	MEXICO Tamps.	15	0.32 - 0.38	0.34	12	0.32 - 0.36	0.34
<i>P. geniculata</i>	MEXICO Morelos	1	0.31		5	0.30 - 0.31	0.305
<i>P. signata</i>	U.S.A. Alabama	8	0.30 - 0.33	0.32			
	U.S.A. Florida	4	0.31 - 0.34	0.32	4	0.31 - 0.32	0.315
	MEXICO Oaxaca	1	0.31		2	0.31	0.31
	PANAMA Paraiso	2	0.30 - 0.32	0.31	3	0.29 - 0.31	0.30

1. See footnotes on Table 13 for additional locality data.

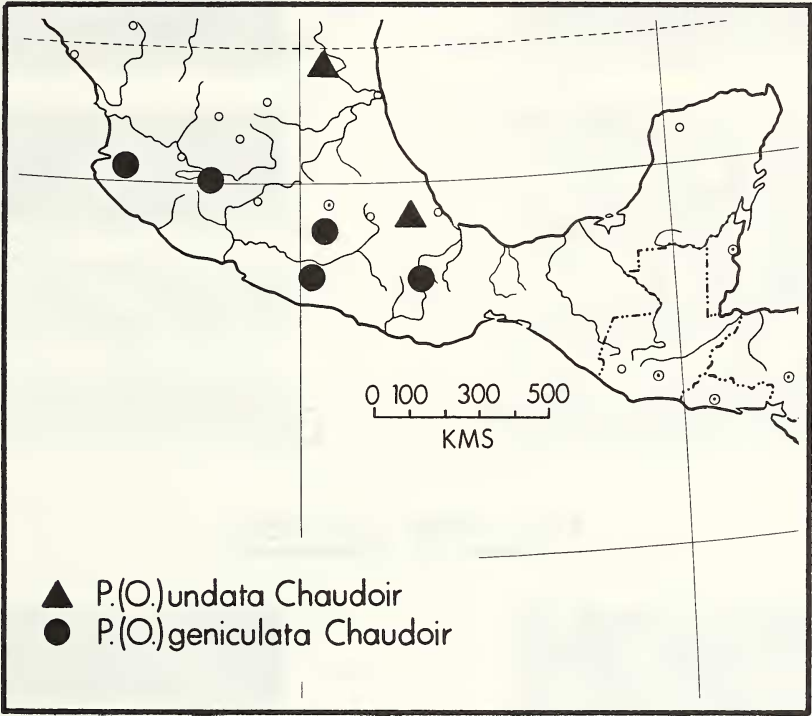


Fig. 103. Map, showing the geographical distribution of *Phloeoxena (Oenaphelox) undata* Chaudoir, and *P. (O.) geniculata* Chaudoir.

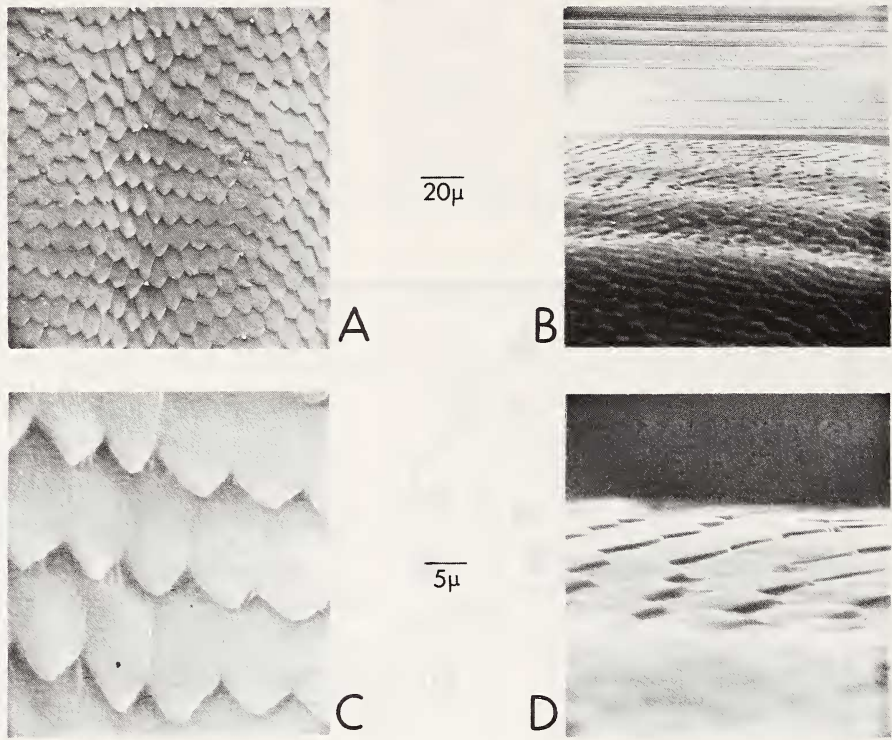
Phloeoxena (Oenaphelox) signata Dejean

Coptodera signata Dejean, 1825: 275. HOLOTYPE male, labelled signata m. in Amer bor [green paper, handwritten] ; Georgia [green paper, handwritten] ; D. Escher [green paper, handwritten] ; collaris LeConte (handwritten); Ex Musaeo Chaudoir [red print] ; in front of this box label — signata Dejean Etats Unis mer. Coll. Dejean [MNHP]. TYPE LOCALITY. Georgia, U. S. A.

ELYTRAL MICROSCULPTURE OF
Phloeoxena signata

DORSAL ASPECT

LATERAL ASPECT



Phloeoxena geniculata

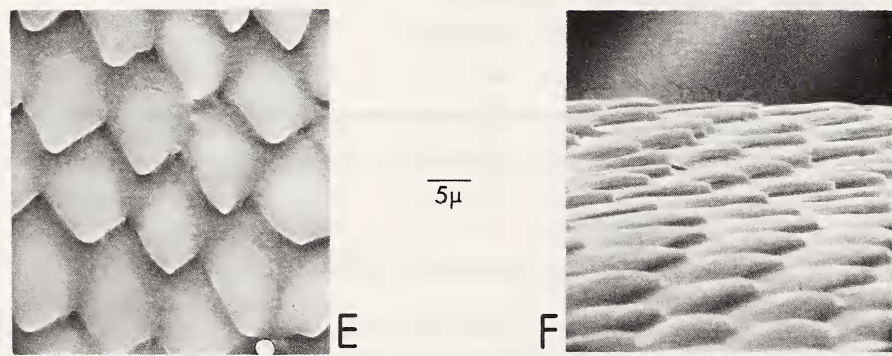


Fig. 104. Stereoscan photographs of elytra microsculpture of *Phloeoxena (Oenaphelox) signata* Dejean and *P. (O.) geniculata* Chaudoir.

Phloeoxena signata; Chaudoir, 1869a: 150. Horn, 1882: 131. Schaupp, 1882: 64. Bates, 1883: 177. — Leng, 1915: 387. — Leng, 1920: 66. — Löding, 1945: 21. — Fattig, 1949: 39. — Kirk, 1969: 16.

Coptodera collaris LeConte, 1848: 197. 4 exx in LeConte Coll, LECTOTYPE female (here selected), labelled: orange disc. Type 5810 [red paper]; *C. collaris* LeC [handwritten]; *signata* 3 [handwritten]. [MCZ]. TYPE LOCALITY. Georgia.

Phloeoxena signata var. *collaris*; Chaudoir, 1869a: 150. — Schaupp, 1882: 64.

Phloeoxena signata var. *nigripennis* Leng, 1915: 587. TYPE LOCALITY. Enterprise, Volusia Co., Florida. NEW SYNONYMY.

Phloeoxena maculicollis Chaudoir, 1869a: 151. HOLOTYPE female in Oberthür Box 126 labelled "Ex Musaeo Chaudoir" [red print], in front of this box label: *maculicollis* Chaud. Nouv Grenade coll. Reiche [MNHP]. TYPE LOCALITY. Colombia or Panama (together they = New Grenada). NEW SYNONYMY.

Phloeoxena hoegi Bates, 1883: 178. LECTOTYPE female (here selected) labelled: Type H.T. [circular label, ringed with red]; Mirador Mexico Hoege; BCA Col. I.i, *Phloeoxena Hoge* Bates; *Phloeoxena Hoge* Bates [handwritten]. (BMNH). TYPE LOCALITY. Mirador, Veracruz, Mexico. NEW SYNONYMY.

Notes on type material and synonymy. — Label data associated with type specimens of *P. signata* Dejean, *P. collaris* LeConte, *P. hoegi* Bates, and *P. maculicollis* Chaudoir, coincide with data in the original descriptions of these forms. I have not seen the type of *P. s. nigripennis* Leng.

The extensive variation in color pattern is sufficient evidence to combine in one species the specimens named *P. hoegi* with those named *P. signata*. By the author's own statement, the type of *P. maculicollis* Chaudoir is hardly different from the type of *P. signata* Dejean, and the main basis given for separating the two was the different places of collection. For details, see below.

Comparisons. — Most specimens of this species are readily distinguished from those of *P. undata* by color of pronotum, which is all pale, or pale with a dark central spot or stripe. Those with a dark pronotum (from Oaxaca) have the elytra clearly bicolored with the pale color predominant in extent. Additionally the dorsal surface is uniformly shining, and spines of the internal sac of the male genitalia are uniformly large.

Description. — Form average for subgenus. Tables 13 to 17 present data on variation in standardized body length and in ratios Hw/Pw, Hw/Pl, P: Aw/Bw and Pl/El.

Color. Piceous black to rufo-flavous, pronotum and elytra various (see below for details). Head black, ventral side of pterothorax and abdomen laterally infuscated. Following rufo-flavous: prosternum and propleura, abdominal sterna medially, antennae, palpi, legs and elytral epipleura.

Microsculpture. Meshes more or less isodiametric, beaded on head, flat on pronotum and elytra (Fig. 104 A-D).

Luster. Head dull, pronotum and elytra shining.

Head. Eyes prominent, bulged.

Pronotum. As in Fig. 105 and 106, transverse; anterior margin moderately concave; lateral margins rounded to slightly sinuate posteriorly, anterior angles prominent, broadly rounded; posterior angles broadly rounded; sides broadly reflexed medially and posteriorly.

Elytra. In form, average for subgenus. Striae shallow, broad, intervals feebly convex, punctuation average for subgenus.

Male genitalia. Median lobe as in Fig. 107-110, curved or straight, apical portion long or short, broad or narrow. Internal sac with 3 to 9 spines, all relatively large for subgenus. Details on variation pattern presented below.

Geographical variation. — Samples are small, so the results presented are tentative. This topic is treated in some detail to provide evidence on which taxonomic decisions were based regarding the status of the different color forms.

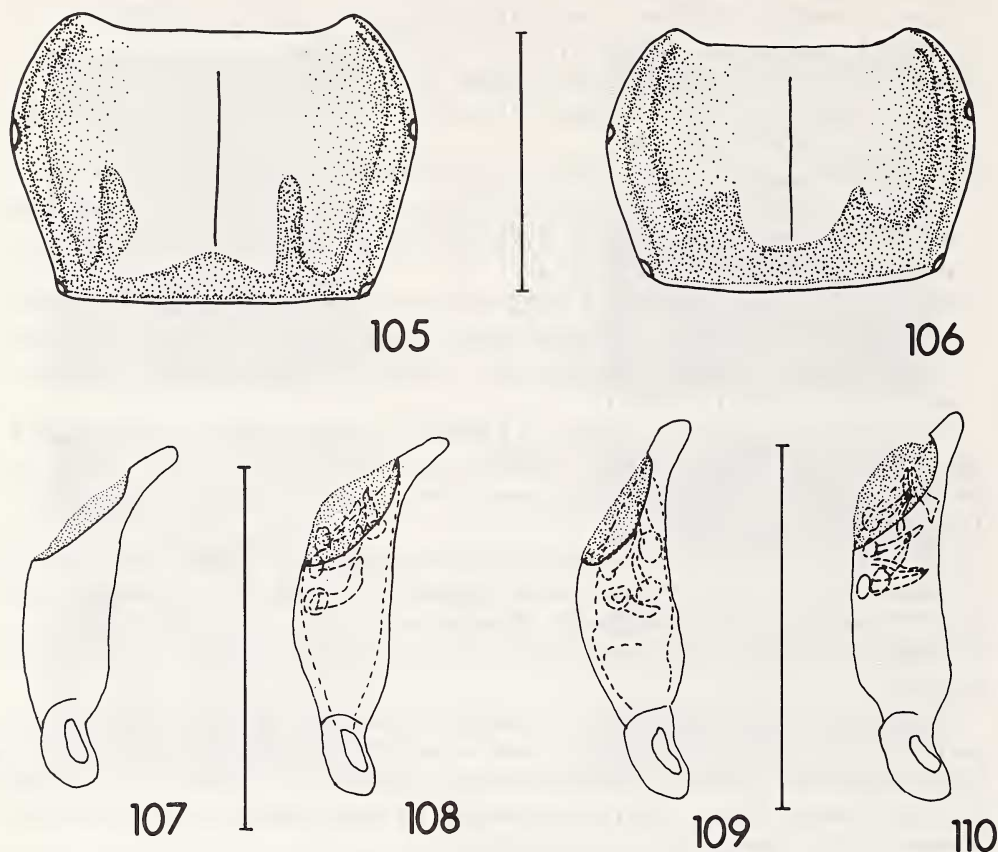


Fig. 105-106. *Phloeoxena signata* Dejean. Pronota, dorsal aspect. Fig. 105. 14.5 mi. s. Juchatengo, Oaxaca. Fig. 106. Ixtapa Jalisco. Fig. 107-110. *Phloeoxena signata* Dejean. male genitalia, median lobes, left lateral aspect. Fig. 107. left lateral aspect (spines of internal sac omitted), Southern Pines, North Carolina. Fig. 108. nr. Ixtapa, Jalisco, with armature of internal sac. Fig. 109. Enterprise, Florida. Fig. 110. 15.4 mi. s. Juchatengo, Oaxaca.

Variation was studied and mapped (Fig. 112) for color pattern of the dorsal surface (Fig. 111 A-H), and form of apex of median lobe (Fig. 107-110), and was noted for standardized body length (Table 13).

For standardized body length the data suggest that larger individuals are commoner in the north than in the south, hence northern population samples have higher mean values than southern ones.

Color pattern is the most conspicuous variable in this species. Color of pronotum and elytra vary independently of one another. In general, the pronotum has a dark median longitudinal stripe, extended from base to apex. Some specimens from Panama, Alabama, and Florida exhibit a central spot because the stripe is not extended the full length of the pronotum. The pronotum is completely pale in specimens from Nicaragua, the Mexican states of Oaxaca (15.4 mi. s. Juchatengo, 34.5 mi. n. Pochutla), Veracruz, Jalisco and Sinaloa, and from Florida in

United States. It is completely dark in three specimens from the Pacific slopes of southern Oaxaca (34.5 mi. n. Pochutla, 13.1 and 21.4 mi. n. Juchatengo).

Elytra color varies from "all dark" to "mostly pale", with dark markings in bicolored specimens consisting of a dark fascia of varying width. The bicolored condition is more widespread, and specimens with completely dark elytra are in peninsular Florida and on the Atlantic Coast of United States. Most bicolored specimens are in the ".50 \pm " class (Fig. 111 D), but in southeastern United States specimens in the ".75 \pm " class (Fig. 111 B) seem to predominate. A specimen from Paraiso, Panama (Fig. 111 E) and four from Oaxaca, Mexico (vicinity of Pochutla and Juchatengo, Fig. 111 F, G and H) have at least the anterior dark markings reduced, and are classified as "mostly pale". (Although the apical area of the elytra of the female from 21.4 mi. n. Juchatengo has an expanded dark marking (Fig. 111 G), it is placed in the "mostly pale" group because of the reduction in the anterior dark areas).

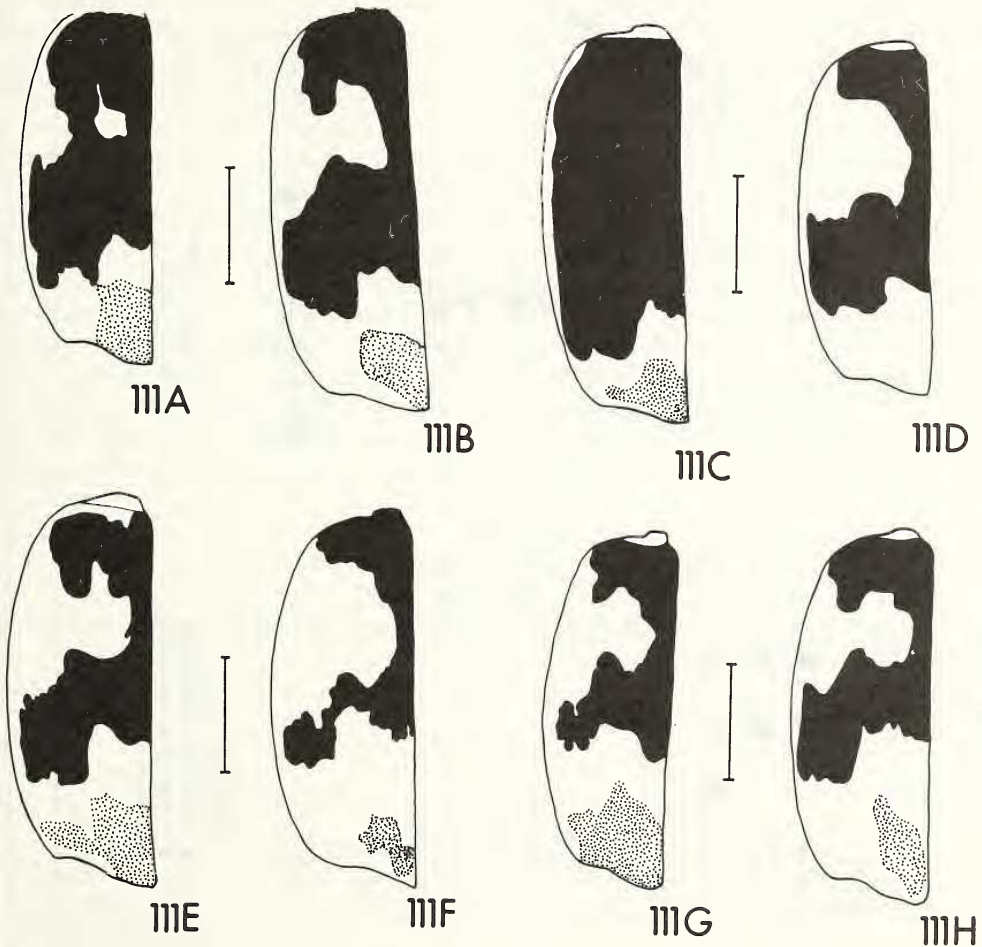


Fig. 111. *Phloeoxena signata* Dejean. Left elytron, color pattern: A and B. Southern Pines, North Carolina; C. Crescent City, Florida; D. nr. Ixtapa, Jalisco; E. Paraiso, Canal Zone, Panama; F. 15.4 mi. s. Juchatengo, Oaxaca; G. 21.4 mi. s. Juchatengo, Oaxaca; H. 34.5 mi. n. Pochutla, Oaxaca.

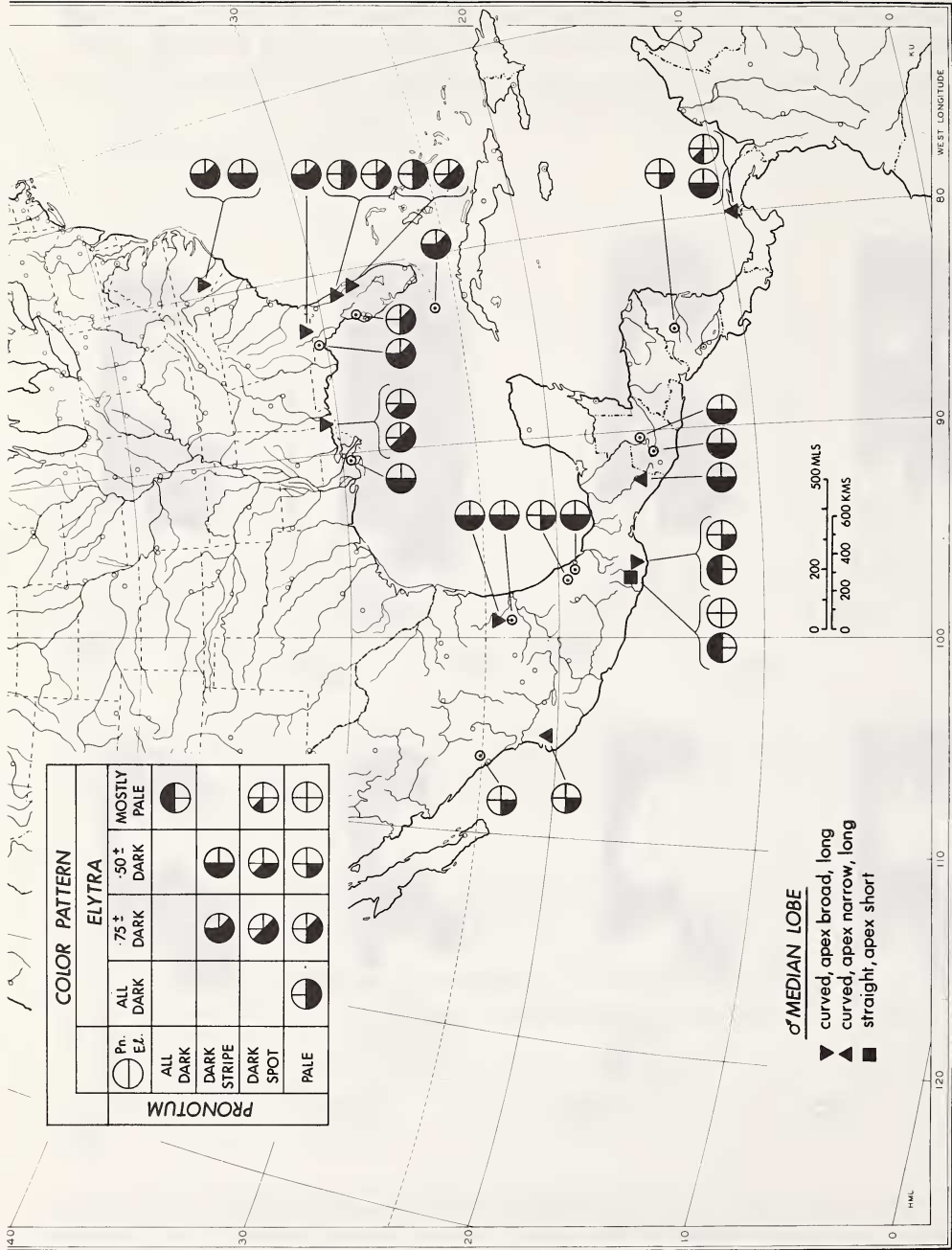


Fig. 112. Map, showing the geographical distribution of *Phloxoxena signata* Dejean, and geographical variation in color pattern of elytra and pronotum.

In combination, the most widespread pattern is pronotum with dark stripe, elytra bicolored, about half dark. In southeastern United States, the elytra are on average darker (normally completely dark in Florida), and the pronotum of most Florida specimens is completely pale. Variation in color may be clinal, the shift toward darker color of elytra occurring along the Gulf Coast in the United States. In contrast, the pronotum becomes completely pale in peninsular Florida, and the transition may be abrupt. However, the specimen from Key West (the island to the southwest of the southern tip of Florida) has a striped pronotum.

In Mexico, color variation is complex. The condition "pale pronotum" is widespread, but too few specimens have been seen to determine if such individuals are members of dimorphic populations, or if the monochromatic condition is characteristic of whole populations. On the Pacific slopes of Oaxaca, the pronotum is darkened and the elytra are lightened in color. Again, too few specimens are available to determine the variation pattern in detail. To the south, both pronotum and elytra tend to have reduced dark pigment.

The male genitalia vary in form of median lobe and in number of spines in the internal sac. There are three forms: 1), median lobe curved, with apical portion long and broad (in United States and Mexico; Fig. 107 and 109); 2), median lobe curved, with apical portion long and narrow (also in Mexico, and southward in Central America, Fig. 108); and 3), the "Oaxacan type", median lobe straight, apical portion short and broad (one ex., Juchatengo, Oaxaca, Mexico; Fig. 110). These three types are not connected by intermediate conditions. The Oaxacan type is the most distinctive. Nevertheless, I think it likely that intermediates between the "curved" and "straight" types will be found, and I think it likely that at least some Mexican populations of *P. signata* will be found to be dimorphic for width of the apical portion of the median lobe.

Number of spines in the internal sac varies from 3 (4.8 mi. n. Frontera, Comalapa, Chiapas, Mexico) to 9 (15.4 mi. s. Juchatengo, Oaxaca, Mexico), with 5 the most frequent (see Table 18). The second highest number of spines is 7, exhibited by a male collected 34.5 mi. s. Pochutla, Oaxaca. Among Middle American specimens (excluding the ones from Oaxaca), the number varies from 3 to 6, and among specimens from United States, the number varies from 4 to 6. Thus, there is essentially no difference between northern and southern males in this characteristic. On the Pacific slopes of Oaxaca, the number of spines is higher. The male with 9 spines has a black pronotum and mostly pale elytra, and the median lobe is straight, with short apex. The male with 7 spines has a pale pronotum and half dark elytra, and the median lobe is curved, with long, broad apex.

Table 18. Frequency Distribution of Number of Spines in the Internal Sacs of Genitalia of Males of *P. (O.) signata* Dejean.

Spine No.	No. Individuals
9	1
8	
7	1
6	2
5	4
4	2
3	1
	<hr/>
	N 11

Synthesis. — A generalized correlation of color characteristics and genitalic characteristics is indicated in Table 19. The pattern can be resolved in terms of four geographical areas: south-eastern United States, Mexico excluding Oaxaca, pacific slopes of Oaxaca, and Central America. In Central America, the elytra are usually bicolored, half dark, pronotum pale or bicolored, the median lobe curved with long, narrow apical portion, and the internal sac with average number of spines.

In Mexico, excluding Oaxaca, the pronotum is pale or bicolored, elytra bicolored, half dark, median lobe curved, with long apex, broad or narrow, and the internal sac with average number of spines. Color variation and form of the median lobe are not correlated. On the Pacific slopes of Oaxaca, there is marked departure from the average pattern of *P. signata*, as well as marked variation: one specimen exhibited the average color pattern for the rest of Mexico, with average form of median lobe, but with 7 spines in the internal sac. Other specimens exhibited dark pronota and reduced elytral markings, highly distinctive median lobe, with 9 spines in the internal sac.

In the southeastern United States, the pronotum is pale or bicolored, elytra overall darker than average, and median lobe curved, with long, broad apical portion.

Taxonomic interpretation. — Evidently the pattern of variation of these characteristics is discordant, suggesting that all of these forms are conspecific. The highly distinctive genitalia of one male from Oaxaca plus the markedly distinctive color pattern of specimens from this area could be taken as evidence that they belong to a species distinct from *P. signata*. However, the male from the Pochutla area that resembles more closely than the others average Mexican *signata* has one more spine in the internal sac than is usual, and thus tends toward the Juchatengo male. This suggests possible clinal variation between the Oaxacan populations and those from the rest of Mexico.

Table 19. Generalized Correlation of Geographical Distribution with Character States of Color and Male Genitalia of *P. (O.) signata* Dejean.

Area or Locality	Pronotum Color	Elytra Color	Median Lobe Form	Apex	Int. Sac No.Spines
USA – Atl. Coast	stripe	.5 - all dark	curved	long, broad	5-6
USA – Florida	pale-stripe	.75 - all dark	curved	long, broad	4-5
USA – Gulf Coast	spot-stripe	.5-.75 dark	curved	long, broad	5
MEX, excl. Oaxaca	pale-stripe	.5 dark	curved	long, broad	
				long, narrow	3-6
MEX Oaxaca, nr. Pochutla	pale dark	.5 dark mostly pale	curved	long, broad	7
MEX. Oaxaca n. Juchatengo	pale dark	mostly pale mostly pale	straight	short, broad	9
GUAT.-PANAMA	pale-stripe	.5-mostly pale	curved	long, narrow	5

Overall, I think the pattern is too complex to be satisfactorily resolved with the material available. Subspecies might be recognized if it is shown that the United States forms are con-

nected to those in Mexico by steep clines, and if the Oaxaca forms are similarly connected to populations from the rest of Mexico. If these conditions were realized, the United States populations would be named *P. signata signata* Dejean, the Middle American ones (excluding Oaxaca) would be *P. s. hoegi* Bates, and a name would have to be proposed for the Oaxacan populations.

Ecological significance of color variation. — The bimaculate pattern may be effective in concealment from predators by disrupting the impression of the outline of the insect. Additionally, the beetles may be members of a complex of Müllerian mimics, for they are marked like many species of *Lebia* occurring in the same area and in the same trees as the ones occupied by the *Phloeoxena* specimens.

The most interesting aspect of the color pattern is its change in detail. Why should the pronotum be dark in Oaxacan specimens, and bicolored or pale elsewhere? Why should the elytra of Florida specimens be dark? Why should the changes occur where they seem to? Answers to these questions are not available now. They might emerge when we know something about the life history of this species.

Notes on habitat. — Specimens have been collected in oak-pine forests in southeastern United States (Leng, 1915: 586) and Mexico, in tropical gallery forests, and in tropical scrub forests, with evergreens and palms. They have been found in bromeliads and beneath pine and oak bark. Kirk (1969: 16) collected specimens on fungus and on chinquipin blooms.

Geographical distribution. — This species ranges from Panama to southeastern United States. In altitude, the range extends from sea level to 6400 feet.

Geographical affinities. — See discussion of this topic in conjunction with descriptions of *P. undata* and *P. geniculata*.

Phylogenetic relationships. — This species is probably most closely related to *P. geniculata*, as indicated in the discussion of relationships of that species. The distribution pattern of *P. signata* is probably plesiotypic, based on the general pattern of tropically-based groups. The uniformly dark pronotum is probably plesiotypic, but the uniformly dark elytra are probably apotypic. Similarly, the bicolored pronotum is probably more plesiotypic than is the completely pale one. The reasoning for these statements is complex, and is developed in the section on evolutionary considerations (p. 226).

The curved median lobe with long, broad apex is probably plesiotypic, and most apotypic is the straight median lobe with short apex. This is based on the supposition that the commoner form of the median lobe in the subgenus is so because of inheritance from a common ancestry.

Localities and material examined. — Seventy eight specimens, from the following localities.

CENTRAL AMERICA

GUATEMALA. San Geronimo (BMNH). Capetillo (BMNH). Miradilla (BMNH). "NICARAGUA" (USNM). PANAMA. Paraiso, Canal Zone. "Nueva Grenada" (MNHP).

MEXICO

CHIAPAS. 4.9 mi. n. Frontera Comalapa, 2400', September 2, 1967 (Ball, Erwin, Leech) (UASM). JALISCO. nr. Ixtapa, gallery forest, under bark of dead tree, 100', December 22, 1970 (G.E. and K.E. Ball) (UASM). OAXACA. Rte. 131, 13.1 mi. n. Juchatengo, 4700', in bromeliads, March 23, 1966 (Ball, McFadden and Whitehead) (UASM). Rte. 131, 21.4 mi. n. Juchatengo, 6400', pine-oak forest, in bromeliads, August 8, 1972 (Ball and Heming) (UASM). 15.4 mi. s. Juchatengo, 5600', in bromeliads, March 22, 1966 (Ball, McFadden, Whitehead) (UASM). 34.5 mi. n. Pochutla, Rte. 175, March 19-20, 1966 (Ball, McFadden, Whitehead) (UASM). SAN LUIS POTOSI. 6.9 mi. w. El Naranjo, October 14, 1965 (Ball and Whitehead) (UASM). SINALOA. Rte. 40, 38.7 mi. n. Concordia, 5000', in bromeliads, January 1, 1966 (Whitehead) (UASM). TAMAULIPAS. Rio Sabinas, w. Encino, 600', in bromeliads, October 11, 1965 (Ball, Whitehead) (UASM). VERACRUZ. Paso de San Juan (BMNH). Jalapa (BMNH).

UNITED STATES

ALABAMA. Mobile, January-February (USNM, MCZ). FLORIDA. Crescent City (Hubbard and Schwarz) (USNM). GEORGIA.

Charlton Co., Billy's Island, Okefinokee Swamp, August 5, 1926 (Coppery) (USNM). LOUISIANA. Bayou Sara (USNM). NORTH CAROLINA. "North Carolina" (USNM). Southern Pines (A.H. Mance) (USNM).

EVOLUTIONARY CONSIDERATIONS

Introduction

Whitehead (1972) explained fully and adequately the justification and rationale for use of the biological species concept and other general aspects of biology related to phylogenetic studies. I subscribe to his views. Here are described simply the working methods used in study of the phylogeny of the species of *Phloeoxena*.

A major shortcoming in the data available for phylogenetic study of *Phloeoxena* is that the material is not sufficiently extensive to warrant detailed analysis. One cannot be sure of the range of variation of character states of each species, nor can one state precisely the geographical affinities of the known species. Additionally, the montane forests of Central America have not been adequately sampled for this genus. Nonetheless, it is essential that each systematic study provide a theoretical basis for further work: a system of hypotheses that can be examined and tested in terms of new information, or other interpretations of existing information (Whitehead, 1972: 307-310).

The objective of phylogenetic analysis is to determine relationships of taxa; that is, the sister groups and their sequence of appearance in time (Hennig, 1966). Sister groups are coordinate members of monophyletic taxa, recognized usually by possession of one or more synapotypic character states. Thus, determination of sister group relationships depends upon a classification of character states such that they can be declared plesiotypic or apotypic.

Ross (1974) has discussed how such a classification can be made, and I summarize here his formulations and explain how I have used them. Conditions of character states are determined by: a. ex-group comparisons, b. in-group comparisons, and c. group trends. Characters themselves can be classified by the number of states represented. More generally, these are few-state or multi-state. A special form of multi-state character is a morphocline (Maslin, 1952).

Ex-group comparisons. — In general, if for a given character, one of its states in one group occurs also in other closely related groups, that state is probably plesiotypic (ancestral). For example, most members of other pericaline genera have two pairs of setae on the pronotum. Within *Phloeoxena*, all species but *P. montana* Darlington have two pairs of pronotal setae. The latter species lacks them; so this character state is probably apotypic and possession of the setae is probably plesiotypic.

A morphocline is a multi-state character whose states, when aligned by some predetermined seemingly logical rule, form a graded series. In ex-group comparisons, one character state of such a graded series is also present in a related group. This is probably the plesiotypic one, as above, for the two-character state. For example, in *Phloeoxena*, there is a 5-state morphocline involving elytral microsculpture, and all of these states occur within the *Phloeoxena schwarzi* group (Fig. 114). The cline involves development of high narrow keels from approximately flat, broad scales. The condition in the specimens of *P. costata* approximates an isodiametric pattern, which is the widespread one for insects generally and hence, thought to be plesiotypic. The other states are more or less apotypic, the most apotypic being that of members of *P. portoricensis*. If one of the intermediate states, rather than one of the ends, is shared with another group, then the morphocline is best interpreted as two clines, each going in a different direction.

Group trends. — In various groups characters appear to follow the same evolutionary development in many independent lineages. For example, in carabids, members of taxa inhabiting high mountain forest tend to lose their wings, shorten the elytra, and lose setae (Darling-

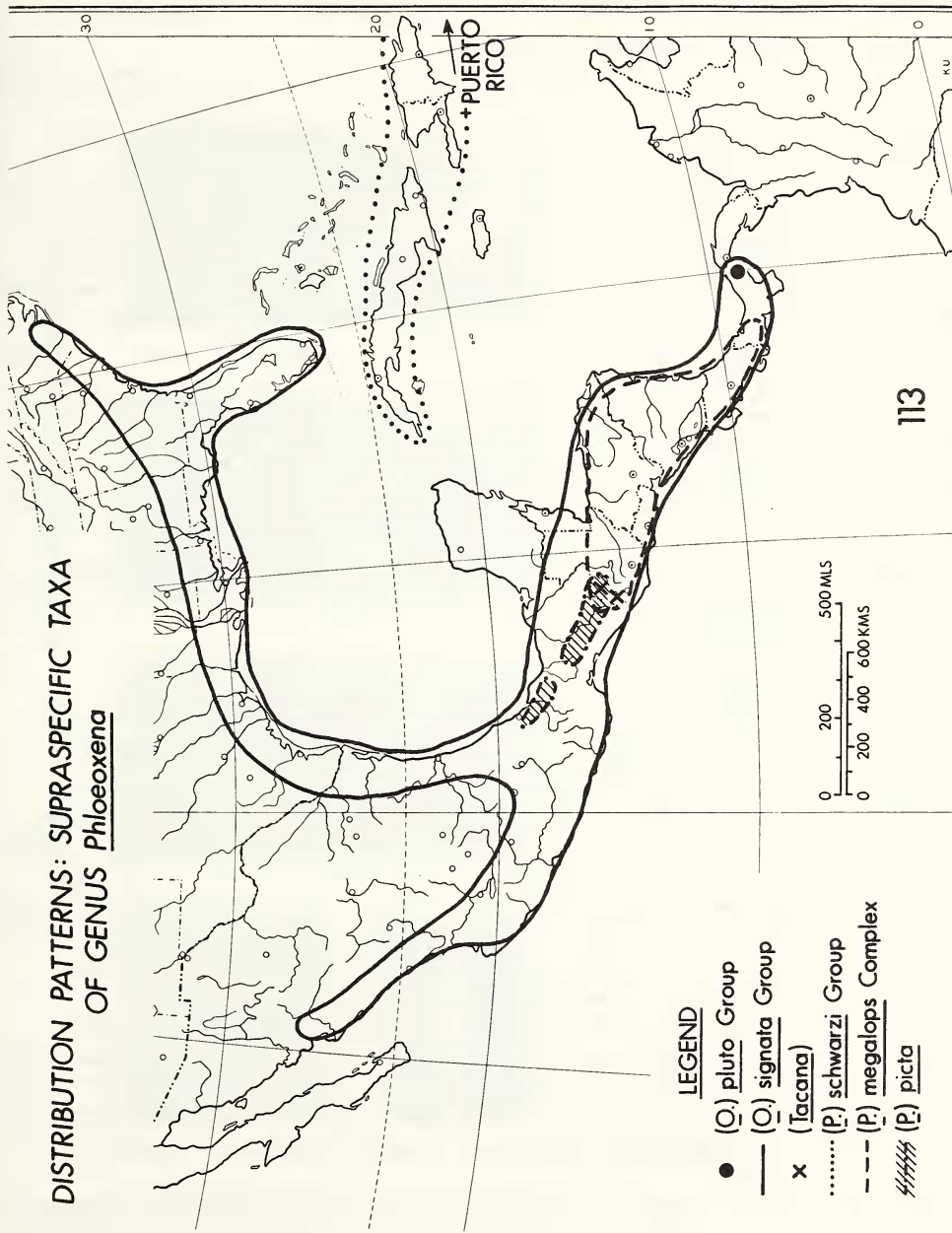


Fig. 113. Map showing geographical distribution patterns of the supraspecific taxa of *Phloeoxena*.

ton: 1971: 165-172; 246-247). On logical grounds, such character states could be interpreted as apotypic in a group not previously analyzed phylogenetically. Specifically, in *Phloeoxena*, wing loss is interpreted as an apotypic character state.

Further, residents of high mountain forests are regarded as descendants of low-altitude stocks (Darlington, 1971: 241), and hence, the former habitat type can be considered apotypic. This principle is applied to the analysis of evolution of *Phloeoxena*.

In-group comparisons. — These involve characters that have arisen within a given group, and thus cannot be compared with those of other groups. One proceeds by determining for an unclassified character which of its states is associated with that member taxon of the complex under consideration judged to be most plesiotypic. Then, this state of the previously unclassified character is judged to be the most plesiotypic.

For example, among members of the *Phloeoxena picta* group, color pattern varies as indicated in the morphocline illustrated in Fig. 115. How is this cline to be read? Is the all dark color of *P. p. unicolor* the most plesiotypic, or is the broadly cruciate pattern of *P. megalops* the ancestral condition? Or, must this state be sought among the other species? As indicated in the diagram, I think that the last choice is the correct one, principally because it is associated with the *P. nigricollis-limbicollis* stock, which is judged to be plesiotypic in body proportions, and which I think to be structurally most plesiotypic of the *picta* group. The reduced coloration is associated with derived forms, inhabiting cloud forests, and the cruciate marking is associated with a lowland form having much enlarged eyes. I believe, then, that evolution of pale color has gone in two directions: reduction in some subspecies of *P. picta*, and increase in *P. megalops*. If one assumed that dark coloration was plesiotypic for this group, then it would have to be, supposed that the same type of color pattern shared by the *P. nigricollis* stock and some members of the *P. picta* stock was developed convergently (or in parallel). This would seem to be a more complex assumption than that of assuming loss of the pale color, which has to happen in a single species only. I feel less sure about regarding the pattern of *P. megalops* as apotypic. Here, I introduce into the argument the coloration of the supposed ancestral stock of the *P. picta* group, which I would suppose to be concolorous. Then, I would imagine development of anterior and posterior pale areas on each elytron, and the gradual increase of the pale color, to give rise ultimately to the condition represented by specimens of *P. megalops*.

Phylogenetic analysis of characters of *Phloeoxena*.

Data presented in Tables 21 and 22 are used in construction of the phylogenetic diagram, Fig. 118. In Table 21, each character is numbered, and each character state is designated by a letter: lower case for plesiotypic, capital for apotypic. Additionally, modifying symbols are provided (superscript letters and numbers) for unrelated states of multi-state characters, or for steps in a morphocline, the numbering being consecutive in relation to relative position of the character state. Table 22 summarizes the character state symbols for each species of *Phloeoxena*. Presented below is the rationale for classification of all character states, and comments on directions of evolution. Because none of the extant pericaline genera known to me seem closely related to *Phloeoxena*, *ex*-group comparisons are necessarily imprecise, being made more with a hypothetical ancestral pericaline than with a particular genus.

Overall size (1). — Plesiotypic condition determined by *ex*-group comparison: generally, members of most other pericaline genera are of about the size of *P. (Tacana) herculeano* specimens. However, within the other subgenera of *Phloeoxena*, I regard the larger size of *P. p. unicolor* specimens as apotypic, because these are cloud forest inhabitants. Thus, I think that the evolutionary pattern involves size decrease early in the history of the genus, followed by increase relatively recently.

Values for Hw/Pl (2). — This is an expression of relative eye size, with small eyes indicated

MORPHOCLINE : MICROSCULPTURE OF ELYTRA

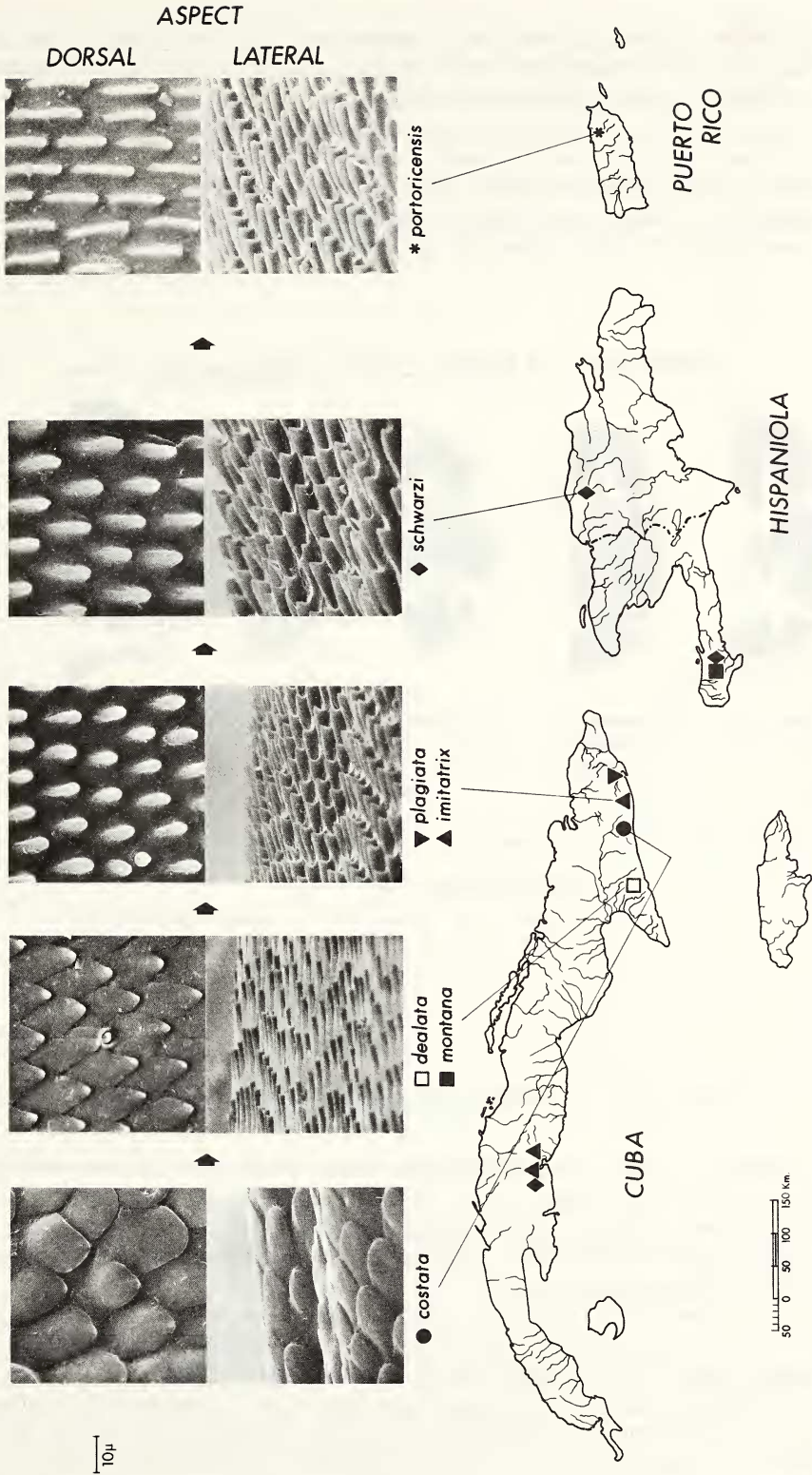


Fig. 114. Map, showing the geographical distribution of species of the *Phloeoxena schwarzi* group, and a morphocline in development of elytral microsculpture.

by low values and large eyes indicated by high values (Fig. 116 and Table 20). Intermediate values are regarded as plesiotypic, both in in-group comparison (of frequent occurrence) and by ex-group comparison (intermediate condition most frequent among pericalines).

Values for Pl/EI (3). — This is an expression of relative length of elytra, low values representing relatively long elytra, and high values representing shorter elytra. The brachypterous species have intermediate and high values, and these are therefore judged to be apotypic on the basis of group trends, because brachyptery is generally regarded as an apotypic character state within most groups of Carabidae. Details are presented in Table 20 and Fig. 118.

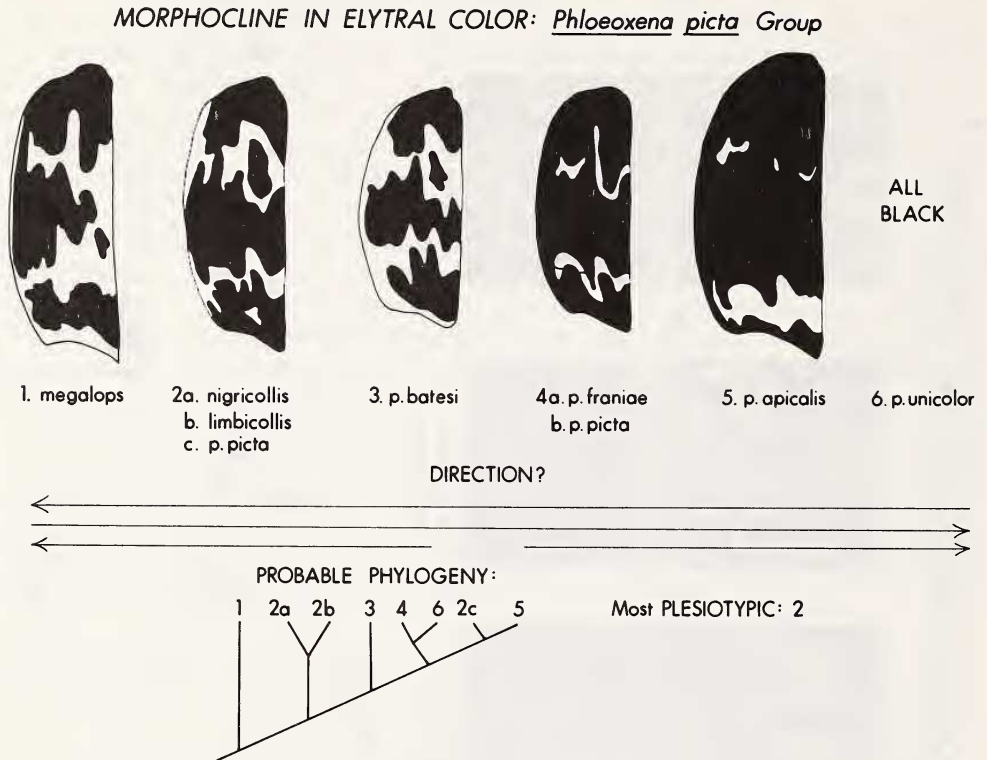


Fig. 115. Morphocline in elytral color pattern among the species of the *Phloeoxena picta* Group.

Reduced eye size and reduce elytral length tend to be correlated and taxa with these conditions tend also to be residents of cloud forests. Conversely, taxa whose members have larger eyes and longer pronota usually live at lower altitudes.

Lateral setae of pronotum (4). — Presence of setae is regarded as plesiotypic on the basis of ex-group comparison (see above).

Color of elytra (5). — This is highly complex. Probably three trends are involved, one going in two directions. The plesiotypic condition is determined by ex-group comparison: in carabids generally, elytra are concolorous. From such a base is evolved character state “E”, appearing in two West Indian species only. A second trend occurs among members of the subgenus *Oenaphelox* with character state E^X (see Fig. 16). In “ E^{X1} ”, the trifasciate condition produces splotches (*P. signata*) and in “ E^{X2} ”, there is a reversion to the plesiotypic condition, or concolorous elytra. Why is not the last-named condition in *P. signata* regarded as plesiotypic? This

is because concolorous elytra appear in populations near the northern periphery of the range of the species (Florida, see Fig. 112). I believe that because the bicolored condition is so widespread, it is simpler to assume that the concolorous condition was secondarily acquired in Florida, from a bicolored stock.

Microsculpture of elytra (6). — A 5-step morphocline is involved (Fig. 115). The plesiotypic state was determined by *ex*-group comparison, and the cline was organized on the assumption of unreversed step-wise change. In Fig. 117 the five steps are indicated by Roman numerals (equivalent to the sequence F-F-F³ in Table 22). Note that state III (F¹) is represented among two groups as is state V (F³).

Table 20

CORRELATION OF GENERALIZED VALUES FOR THE RATIOS Hw/Pl AND Pl/El FOR THE SPECIES OF <u>Phloeoxena</u>					
decrease in elytral length ↓	Pl/El	increase in eye size → Hw/Pl			
		low	int.	high	
	low		costata (2) plagiata (2) schwarzi (2)	nigricollis (3) limbicollis (3)	pluto (5) signata (5) geniculata (5) portoricensis (2)
	int.		dealata (2) montana (2) imitatrix (2)	undata (5) p. batesi (4)	
high		herculeano (1)	p. franiae (4) p. unicolor (4) p. picta (4) p. apicalis (4)		
		APOTYPIC	← PLESIOTYPIC →	APOTYPIC	

Umbilical series of setigerous punctures of elytra (7). — Of the two recognized states, the plesiotypic was determined by *ex*-group comparison: the commonest condition among pericalines is to have relatively few punctures in this series, with a broad diastema between a basal and an apical group.

Discal setigerous punctures of elytra (8). — Three states are recognized, with three punctures regarded as plesiotypic and more than this ("H⁺"), or less than this ("H⁻") being apotypic. The basis is *ex*-group comparison, with three being the number common to many pericalines. Hence, the proposed evolutionary trends are self-evident.

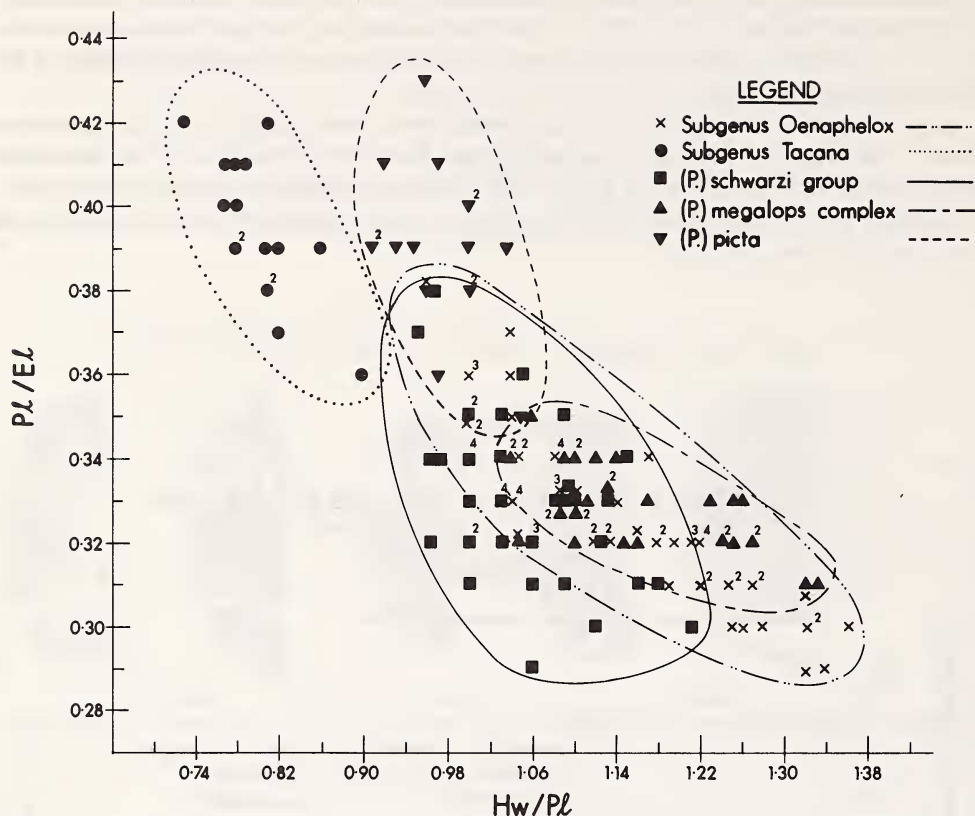


Fig. 116. Graph showing relationship of variation in the ratio Pl/EI and Hw/Pl among the species of *Phloeoxena*.

Elytral striae (9). — The plesiotypic condition was determined by ex-group comparison. There are two trends: one, to broadly costate striae (J^+), and one to a reduction in striae, with several steps involved (J , J^1 and J^2).

Internal sac of male genitalia (10). — The plesiotypic condition of this 4-step morphocline was determined by ex-group comparison: in pericalines generally, spines are lacking from the internal sac. Orientation of the morphocline was based on the assumption that spines increase in size and number in step-wise fashion, more or less.

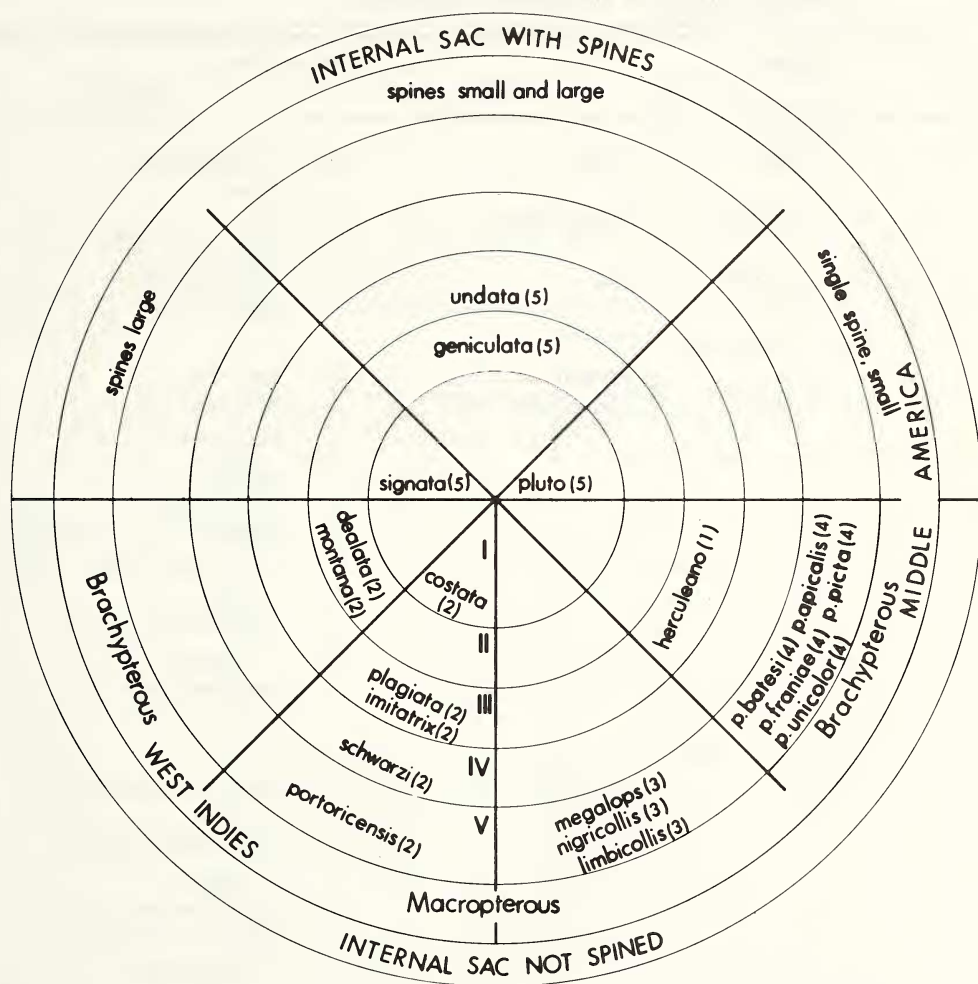
Construction of the phylogeny

This was carried out by search for clusters; definition of clusters to form provisional groups; determination of intra-group relations by analysis of morphoclines; and then, determination of inter-group relations.

Search for clusters. — Fig. 117 and Table 20 indicate certain general correlations, and in combination, they give the defining characters for provisional groups.

Clusters. — There are five, as indicated by the numbers following names in Table 20 and Fig. 117.

Group 1: large size, small eyes, relatively short elytra, moderately derived microsculpture and extra elytra punctures.

SPECIES OF PhloeoxenaCORRELATION DIAGRAM FOR CHARACTER STATES OF ELYTRAL
MICROSCULPTURE, INTERNAL SAC, WING DEVELOPMENT
AND GEOGRAPHICAL DISTRIBUTION

MICROSCULPTURE DEVELOPMENT

- I - plesiotypic
- II, III, IV - intermediate
- V - highly apotypic

Fig. 117. Correlation diagram for character states of elytra microsculpture, armature of internal sac of male genitalia, wing development and geographical distribution (in part) among the species and species groups of *Phloeoxena*.

Group 2: small size, and confined to West Indies; otherwise no synapotypic character states. This group is based on the assumption that the West Indian area was invaded only once, and considering the overall closeness of the species to one another, this seems reasonable.

Group 3: elytral microsculpture highly apotypic and color pattern apotypic.

Group 4: a single polytypic species, well defined by short eyes and relatively short elytra (result of brachyptery), and inhabiting tropical montane or cloud forests.

Group 5: well defined by spined internal sac, generally large eyes and generally long elytra.

Table 21. Phylogenetic Classification of Character States used in Reconstruction of the Hypothetical Phylogeny of the Species of *Phloeoxena*.

No.	Character	Character State	
		Plesiotypic	Apotypic
1	Overall size	large a	intermediate A ¹ small A
2	Value for Hw/Pl	intermediate b	low B ⁻ high B ⁺
3	Value for Pl/EI	low c	intermediate C high C ¹
4	Pronotum: lateral setae	present d	absent D
5	Elytra: color	concolorous, dark e	single red spot E trifasciate E ^x splotch E ^{x1} uniformly dark E ^{x2} bifasciate, w/ant. dark spot. E ^y bifasciate, w/o ant. dark spot E ^{y1} bifasciate, ant. fascia broken E ^{y2} uniformly dark E ^{y3} broadly cruciate E ^{+y}
6	Elytra: microsculpture	meshes flat scales f	scales slightly elevated, broad F scales more elevated, ridged F ¹ ridges narrower, higher F ² ridges in discrete, longitudinal rows F ³
7	Elytra: punctures, umbilical series	broadly interrupted g	continuous G
8	Elytra: punctures, discal series	3 h	4-8 H ⁺ 2 H ⁻¹

Table 21. (concluded). Phylogenetic Classification of Character States used in Reconstruction of the Hypothetical Phylogeny of the Species of *Phloeoxena*.

No.	Character	Character State	
		Plesiotypic	Apotypic
9	Elytra: striae	narrow, clearly marked . . . j	broad, clearly marked J ⁺ broad, faintly marked J only stria 7 evident J ¹ all obliterated J ²
10	Male genitalia, internal sac	not spined k	single small spine K small and large spines K ¹ large spines, only K ²

Table 22. The Species-Group Taxa of *Phloeoxena*, Their Characters and Character States, Classified Phylogenetically.

Name of Taxon	Character									
	1	2	3	4	5	6	7	8	9	10
<i>herculeano</i>	a	B ⁻	C ¹	d	e	F ²	G	H ⁺	j	k
<i>costata</i>	A	b	c	d	e	f	g	h	J ⁺	k
<i>dealata</i>	A	b	C	d	e	F	g	h	J	k
<i>montana</i>	A	b	C	D	e	F	g	H ⁻	J	k
<i>plagiata</i>	A	b	c	d	E	F ¹	g	h	J	k
<i>imitatrix</i>	A	b	c	d	E	F ¹	g	H ⁻	J	k
<i>schwarzi</i>	A	b	c	d	e	F ²	g	h	J ¹	k
<i>portoricensis</i>	A	B ⁺	c	d	e	F ³	g	h	J ²	k
<i>megalops (s. lat.)</i>	A	B ⁺	c	d	E ⁺ y	F ³	g	h	J	k
<i>limbicollis</i>	A	b	c	d	E ^y	F ³	g	H ⁻	J	k
<i>nigricollis</i>	A	b	c	d	E ^y	F ³	g	h	J	k
<i>p. batesi</i>	A	b	C	d	E ^y	F ³	g	h	J	k
<i>p. franiae</i>	A	b	C ¹	d	E ^y 1	F ³	g	H	J	k
<i>p. unicolor</i>	A ¹	b	C ¹	d	E ^y 3	F ³	g	h	J	k
<i>p. picta</i>	A	b	C ¹	d	E ^y	F ³	g	h	J	k
<i>p. apicalis</i>	A	b	C ¹	d	E ^y 2	F ³	g	h	J	k
<i>pluto</i>	A	B ⁺	c	d	e	f	g	h	J	K
<i>undata</i>	A	b	C	d	E ^x	F ¹	g	h	J	K ¹
<i>geniculata</i>	A	B ⁺	c	d	e	F	g	h	J	K ¹
<i>signata</i>	A	B ⁺	c	d	E ^x 1 E ^x 2	f	g	h	J	K ²

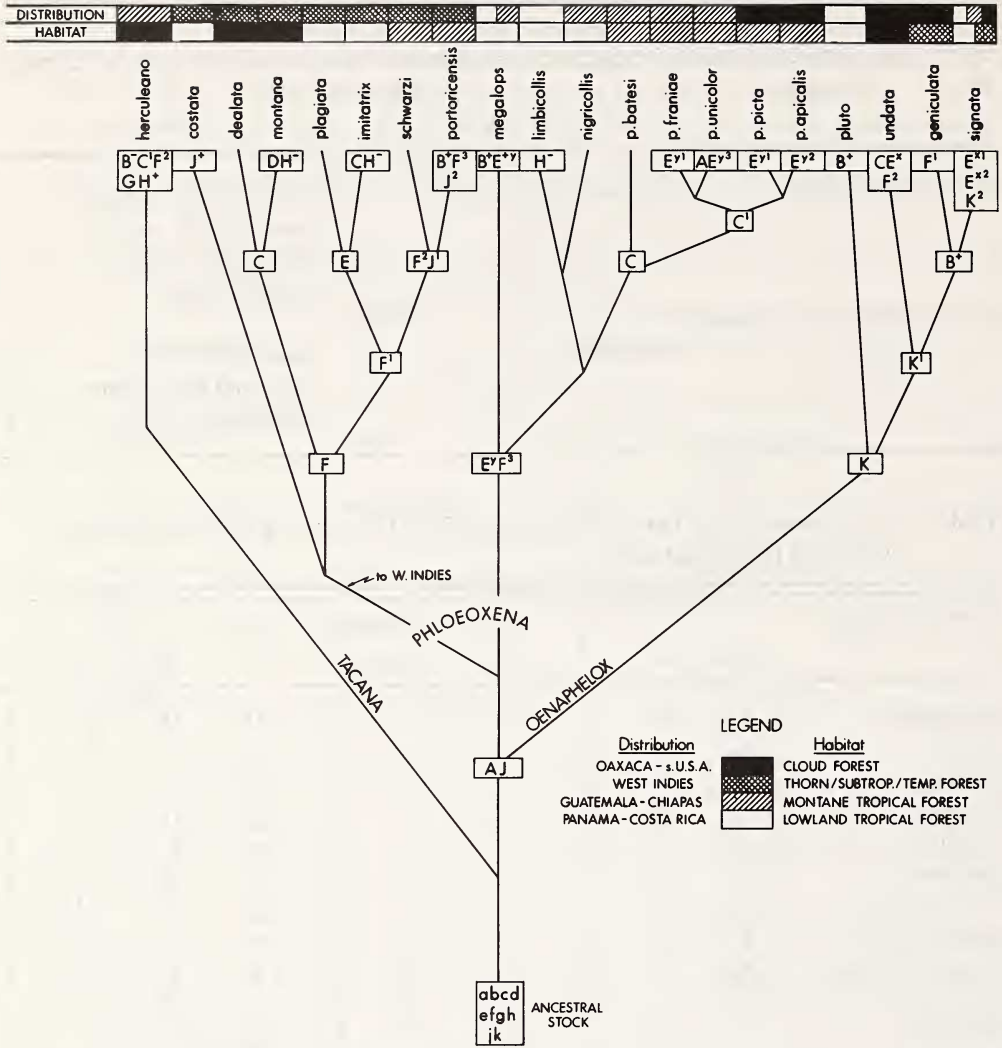


Fig. 118. Diagram illustrating the reconstructed phylogeny of the species of the genus *Phloeoxena*.

Intra-group relationships. — These are derived by study of morphoclines.

Group 1: *P. herculeano* stands by itself.

Group 2: the axis of species orientation is mainly the morphocline for elytra microsculpture, but partly, geography (Fig. 114): the species with the most highly derived microsculpture is on the most remote island. Also, this system is paralleled by one for eye size (greatest in the Puerto Rican species), and for development of the elytral striae (specimens of *P. portoricensis* with completely smooth elytra; *P. schwarzi* between *P. portoricensis* and the rest of the West Indian species both in development of striae and in geography).

Group 3: the main axis is the morphocline for eye size and color, but *P. megalops* with apotypic color pattern and large eyes is regarded as closest in time of origin to the ancestral stock of this group. This is based on the seeming close relationship between the highly derived *P. picta* and the *P. nigricollis-limbicollis* stem, on the remoteness of *P. megalops* from *P. picta*,

and on the primitiveness of *P. megalops* in features other than eye size and color.

Group 4: the system of relationships is based on degree of geographical proximity, and the morphocline is oriented on geographical grounds, with the assumption that the southernmost (*P. p. batesi*) subspecies is likely to be closest to the ancestral stock, and the northernmost one the most derived.

Group 5: the morphocline for spine development of the internal sac seems to provide a guide to understanding phylogeny of the group. Basally is *P. pluto*, in a group of its own, with small spines, and geographically remote from the others. Then, is *P. undata* and *geniculata*, with small and large spines; finally, is *P. signata*, with all large spines. Associated with this trend in the *signata* group is one for enlarged eyes, and broadening of the pronotum. Clearly, the most primitive member of this group is *P. undata*. Note, however, that the morphocline for elytral microsculpture is the reverse of what one would expect, *a priori*. I assume that the *P. undata* and *P. geniculata* stocks acquired the apotypic condition independently.

Inter-group relationships: the search for sister groups. — Probably the sister group to all the others is the subgenus *Tacana* (*P. herculeano*). It is structurally quite remote, is plesiotypic with respect to size, and has a relict distribution. Thus, it is likely to be a highly derived member of an old stock.

Of the remaining groups, *P. picta* is clearly an apotypic descendant of the *P. megalops* "complex"; there is no need to formally recognize another taxonomic level, so the combination of Groups 3 and 4 is called simply the *P. picta* group. The sister group of the generally more plesiotypic *schwarzi* (2) and *picta* groups is Group 5, which is clearly isolated by possession of the spines of the male internal sac. Unfortunately, there are no synapotypic features to link the *P. schwarzi* and *P. picta* groups, but I feel confident that such will be found in some character system that has yet to be investigated.

Convergences

The above account deals mainly with evolutionary divergence from common ancestors. However, not all character states of related extant taxa are unique or evolutionarily unreversed. In phylogenetic studies, it is important to note similarities apparently not the result of descent from a common ancestor; such similarities give clues to the major selective forces at work on members of the genus and might give clues to other interpretations of relationships. There seems to have been one reversal in size development, with *P. p. unicolor* being larger than any other member of the genus except those of *P. herculeano*. Eyes have undergone increase in size four times (once each in the *schwarzi*, *picta*, *pluto* and *signata* groups). The elytra have shortened markedly twice (once each in *Tacana* and the *picta* group), and moderately four times (twice in the *schwarzi*, once each in the *signata* and *picta* groups). In color pattern, the elytra have become fasciate twice (*signata* and *picta* groups), and pale color has been lost twice (once each in the *picta* and *signata* groups). The elytral microsculpture has become keeled five times (once each in *Tacana*, *schwarzi* and *picta* groups, and twice in the *signata* group). The keels have become high and linearly arranged twice (once in the *picta* and *schwarzi* groups).

Zoogeography

The pattern. — This is illustrated in broad outline by Fig. 113. Briefly, maximum diversity occurs in the Chiapas-Guatemala area, where the following taxa are represented: subgenus *Tacana*; *picta* group (*megalops* complex and *P. picta*); and *signata* group. The *schwarzi* group is confined to the West Indies, and the *pluto* group is known only from Panama. The extensive range of the *signata* group results from the wide distribution of *P. signata* (Fig. 112). The other two species of this group are known only from Mexico north of the Isthmus of Tehuantepec, and it is in this area that *P. signata* is maximally divergent. The northernmost species of the

picta group, *P. picta*, occurs on both sides of the Isthmus of Tehuantepec. In general, then, most of the species are confined to Middle America, with the range of one species extending to southeastern United States, and one group being confined to the West Indies.

The distribution of the West Indian fauna forms a classical subtraction pattern, with the smallest island and the one farthest from the mainland (Puerto Rico) having only a single species, the middle-sized and geographically intermediate Hispaniola having two species (one shared with Cuba), and the island closest to the mainland and largest in area (Cuba) having five species. Darlington (1957: 510-515) discusses such a pattern at length.

Ecological affinities, a second parameter of the pattern, are indicated in terms of generalized forest types. Seven species are in relatively lowland tropical forest, three in montane tropical forest, four in cloud forest, one in thorn-subtropical forest, and the range of *P. signata* extends from warm temperate hardwood forest through subtropical forest to lowland tropical rain forest. In terms of numbers of species, maximum diversity of *Phloeoxena* is in the lower elevation tropical forests, although in combination the high altitude forests have as many species as the former habitat.

A third parameter concerns vicariance relations. These are important in interpreting zoogeographic patterns; their value increases in proportion to extent of knowledge of species ranges. Because distribution data for *Phloeoxena* are so limited, this parameter cannot be considered in detail. In general, the species seem to be mainly parapatric or allopatric, although in Cuba *P. schwarzi* and *P. imitatrix* are almost certainly sympatric.

This pattern should be viewed in conjunction with the general distribution pattern of the New World pericalines. All other genera (except *Ochropisus*, whose three known species are confined to Middle America) are maximally diverse in South America. All genera, except *Oreodicastes* occur in Middle America, but the range of only one (*Coptodera*) reaches southern United States.

Historical zoogeography. — A generalized scenario is presented, as an initial attempt to explain the distribution pattern described above.

The relative abundance of pericalines in South America as contrasted with Middle America can provisionally be accepted as evidence that the larger continent was the principal theater of evolution of this subtribe in the New World, and probably served as the source area for the ancestral stock of *Phloeoxena*. This is an extraordinarily common pattern, as discussed by a variety of authors for a variety of groups (recently published examples are: Duellman, 1970 — hylid frogs; Savage, 1973 — anurans, generally; Whitehead, 1972, Noonan, 1973 and Goulet, 1974 — carabid beetles).

Following the arguments of Whitehead on rates of evolution (1972: 334-335), differentiation of the extant lineages of *Phloeoxena* probably began not less than 21 million years before the present (BP), or in mid-Miocene time. Thus, it is important to know about palaeogeographic events of the Tertiary period for the "circum-Caribbean" area (Ross, 1967: 196), where evolution of *Phloeoxena* took place.

Geological events are complex, but in mid-Tertiary time nuclear Central America comprised Mexico south of the Isthmus of Tehuantepec, Guatemala, Honduras, El Salvador and Nicaragua only, and was isolated from South America by a sea gap which probably contained a series of islands volcanic in origin (Malfait and Dinkelman, 1972: Fig. 3). By the end of the Pliocene, nuclear Central America was joined by lower Central America to South America.

According to Durham et al. (1955), the Isthmus of Tehuantepec at this time was not a sea-way, so nuclear Central America was a southern extension of North America. However, the connection may have been a very tenuous one, for the sea extended from the Gulf of Mexico across most of what is now the Isthmus, to the low hills in its southern part. One might well imagine that, generally, habitats in the vicinity of the Isthmus would not have been favorable

for forest adapted species of organisms, and the area might have served as a barrier for dispersal. Thus, for biogeographic purposes, nuclear Central America might have been ecologically isolated from the rest of North America, and may have been effectively an island (as suggested by many authors – for example, Darlington, 1957: 280 – Maldonado-Koerdell, 1964: 15, and Fig. 8; – Ross, 1967: 195-196).

The geological history of the West Indies is also complex, but there is no clear evidence that the islands were connected to one another by land, nor that they were connected to the circum-Caribbean mainland (Malfait and Dinkelman, 1972). The maps of Maldonado-Koerdell (1964), (reproduced by Ross 1967, Fig. 12, 13 and 14) seem to be without a firm geological foundation. Nonetheless, the sylvan fauna is sufficiently diverse and divergent to suggest that a land connection to Central America existed (Hershkovitz, 1972: 337). Probably the zoological and geological data can be rationalized by postulating for some time in the mid-Tertiary more favorable conditions for overseas dispersal than is suggested by the present distribution of land and sea.

Two of the three subgenera of *Phloeoxena*, *Tacana* and *Phloeoxena (sensu stricto)*, are represented in nuclear Central America by endemic species. I postulate that the group arose there, derived from a South American ancestor that managed to move northward from island to island, across the Bolivar geosyncline and other narrow sea gaps (Fig. 119). Differentiation took place in response to geographical isolation and changing conditions wrought by mountain-building and consequent alterations to the environment. The earliest stock to evolve, represented today by a single cloud forest species, *P. herculeano*, was probably displaced from lowland forests, but succeeded in adapting to and surviving in montane cloud forests.

The stock ancestral to the nominotypical subgenus and *Oenaphelox* (Fig. 119), whose evolution may have displaced the *Tacana* stock from the lowlands, became widespread probably in Miocene time, one lineage developed whose males had a single small spine in the internal sac, and dispersed northward to southern North America, and eventually south to Panama, too. This was the ancestral stock of *Oenaphelox*, which is represented in southern tropical forests by *P. pluto*. Still later, that portion of the stock that succeeded in crossing the Isthmus of Tehuantepec differentiated to produce the *signata* group ancestor (Fig. 120).

The history of the southern *pluto* group cannot be pursued farther, because its only known species is represented by a single specimen. But the history of the northern group is worth further consideration. Details of the process of differentiation are unclear, but I believe that a lowland stock gave rise, first, to the ancestor of *P. undata*, represented today by cloud forests populations only. Further differentiation in the lowlands gave rise to the ancestor of *P. geniculata* and *P. signata*, with the former species becoming confined to western Mexico, in thorn forest, or other subtropical formations. On the other hand, *P. signata* became very widespread, ranging northward to southeastern United States and southward throughout Central America. This species underwent marked differentiation near its center of origin, in Oaxaca, and less differentiation in eastern United States (pp. 216-222, Fig. 105-112).

Implicit in this proposed dispersal pattern is the idea of apparent extinction of the ancestral stock of *Oenaphelox* in nuclear Central America. Now, of course, the group is represented therein by *P. signata*, but I suggest that is the result of relatively recent dispersal from the north (Fig. 120). Further, I suggest that the extensive distribution of *P. signata* can serve as a model for events in the early history of the subgenus, with the ancestral stock becoming widespread, and then undergoing differentiation.

Returning to nominotypical *Phloeoxena*, the sister group of *Oenaphelox* in nuclear Central America, the former group became widespread within the confines of that area, eventually dispersing across the sea to Cuba (possibly by way of Jamaica, although no species of the genus are currently known from that island). The mainland stock differentiated, to become the *picta*

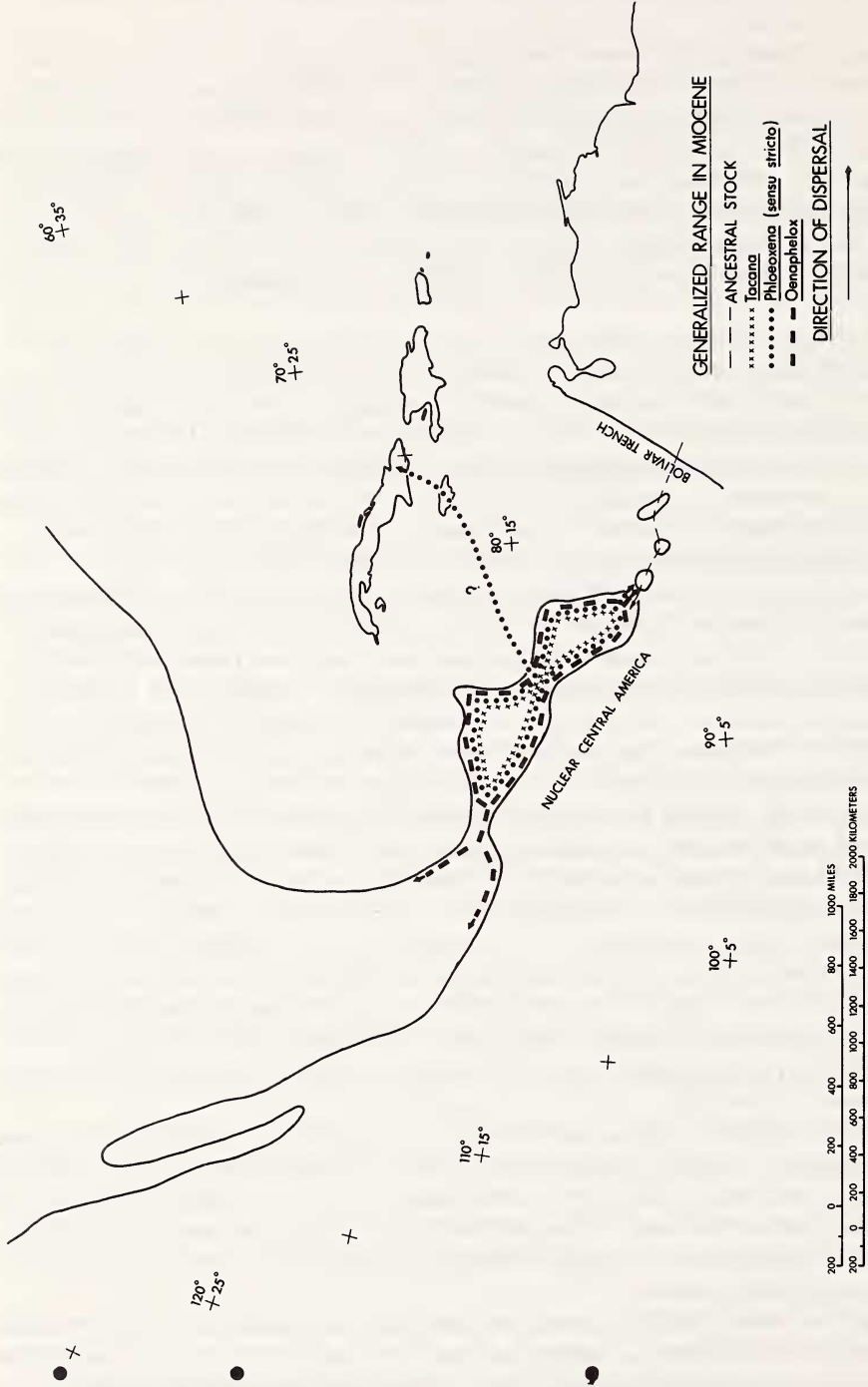


Fig. 119. Map showing the hypothetical Miocene distribution and form of Middle America and adjacent parts of North and South America, and hypothetical dispersal and distribution of the taxa of *Phloeoxena* during the Miocene.

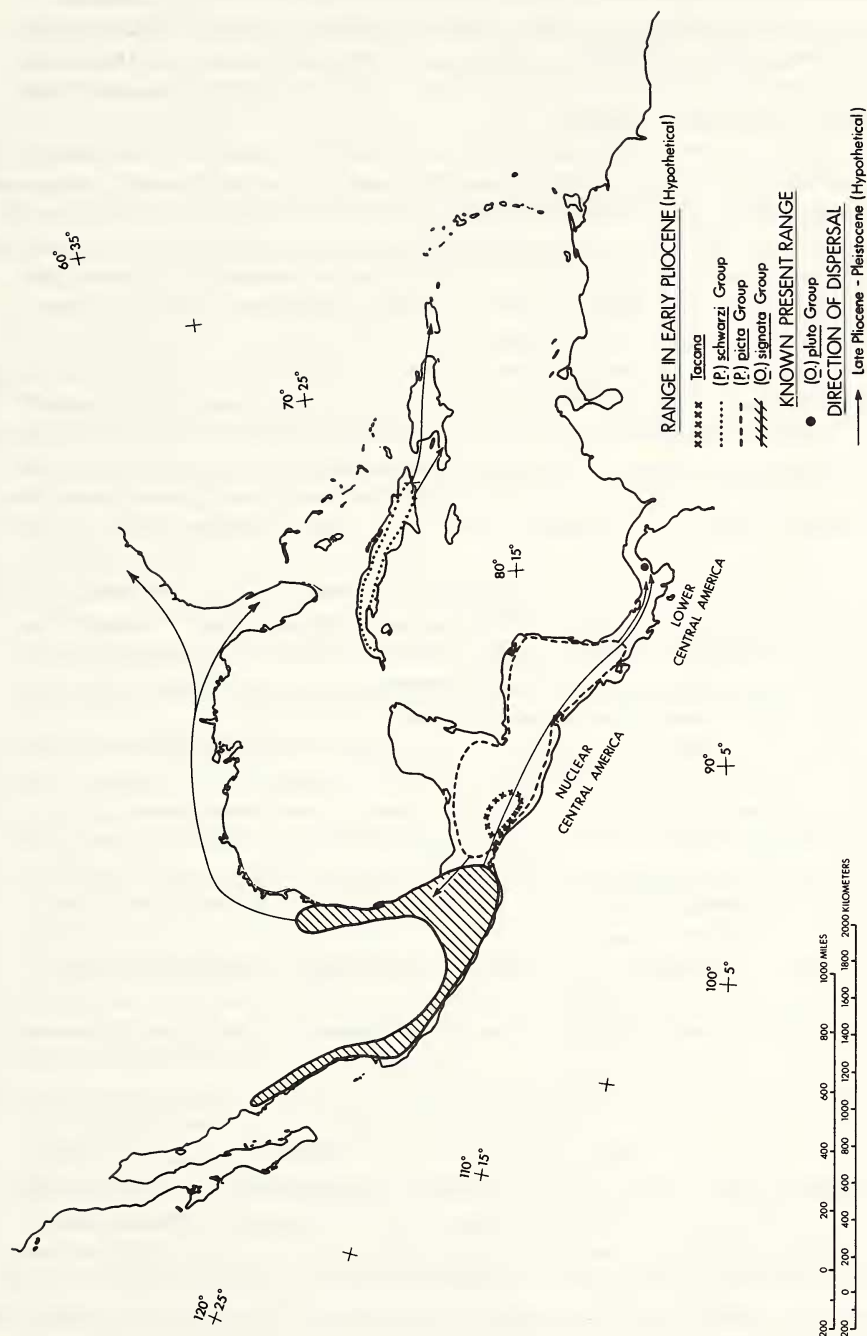


Fig. 120. Map showing the hypothetical dispersal and distribution of the taxa of *Phloeoxena* from Pliocene to Recent.

group and the islandic stock became the *schwarzi* group (Fig. 119 and 120).

Evolution of the *schwarzi* group took place mainly on Cuba, with one stock reaching Hispaniola (possibly when the two islands were still joined) and differentiating (*P. dealata* on Cuba and *P. montana* on Hispaniola). Later, another stock spread eastward to Puerto Rico, and differentiated, with the plesiotypic sister species (*P. schwarzi*) on Cuba and Hispaniola, and the apotypic one (*P. portoricensis*) on Puerto Rico (Fig. 120). Differentiation on Cuba led to evolution of cloud forest species.

The evolutionary pattern of the *picta* group is more difficult to decipher. The macropterous lowland forms are generally more southern than is the montane *P. picta*. Evidently, in the course of its evolution, southern North America was not an important center, and may have been invaded comparatively recently (the only species represented north of the Isthmus of Tehuantepec is the brachypterous montane forest-adapted *P. picta*). What seems most likely is a southern dispersal of the *P. picta* stock, possibly when land in Central America consisted of a chain of islands, followed by differentiation on different islands (Fig. 120).

This pattern is similar to the one suggested by Goulet (1974) for the evolution of the temperate-adapted harpaline genus *Pelmatellus*. Both this genus and *Phloeoxena* probably arose from South American ancestors, dispersed northward across water barriers to nuclear Central America (Goulet's "Guatemalan mountains") underwent important differentiation there, and spread north and south, and upward into cloud forests, where members of both groups became brachypterous. The pattern differs in that *Pelmatellus* is not represented in the West Indies, nor at low elevations.

This pattern is also similar to the one suggested by Duellman (1970) for the history of hyliid frogs of Middle America, differing only in that the diversity of the beetles is much less than that of the frogs. For the New Guinea Carabidae Darlington (1971: 239) described the same pattern, with successive groups arising in the low altitude forests, and subsequently invading the higher altitudes, and being displaced in the lowlands.

Finally, a comment seems in order about the general question of the derivation and nature of the Middle American fauna. Darlington (1957: 574-575) emphasized its transitional nature, suggesting that it was derived in part by subtraction from the more recent elements of the main Nearctic and Neotropical faunas, and was in part an accumulation of earlier megagean groups that had succeeded in dispersing from the Old World Tropics, had been mainly replaced to the north, and had been denied access to South America by the highly diverse endemic fauna that had developed from still earlier waves of megagean groups. No doubt the Middle American fauna is in part the result of subtraction from the more extensive northern and southern faunas. But the element ascribed to "accumulation" is probably mostly of South American derivation and represents groups that in early Tertiary time succeeded in crossing water gaps and thus reaching relatively extensive nuclear Central America, undergoing isolation and marked differentiation there, followed by dispersals both northward and southward. This pattern is seen most clearly in hyliid frogs (Duellman, 1970 — although the author suggested the ancestral stocks of the nuclear Central American fauna reached there over land, in the belief that North and South America had been joined prior to the later Pliocene). It is suggested by what is known about the carabid groups *Pericalina* and *Pelmatellus*, and is probably seen also in the distributions of those mammalian groups that succeeded in entering South America between Oligocene and Pliocene time (Hershkovitz, 1972). Thus, in addition to serving as a link or "highway" for dispersal between two continents, Middle America has been a major New World center of evolution (Ross, 1967: 195).

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Hans Reichardt (Museu da Universidade de Sao Paulo, Brasil) reviewed the penultimate manuscript of this paper, and drew to my attention the description of *Catascopellus* Straneo, a genus I had overlooked.

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Members of the staff of my Department rendered assistance as follows. Stereoscan preparations and photographs were made by Margaret Abraham and George Braybrook, respectively. John C. Scott made the other photographs and prepared all of the plates. Preliminary drafts of the manuscript were criticized by my colleagues Gerald R. Noonan and Douglas A. Craig. The final draft was typed by Twyla E. Gibson.

Additionally, George Braybrook suggested that we examine in lateral aspect the elytral microsculpture of the *Phloeoxena* specimens, thereby contributing literally as well as figuratively a new dimension to understanding the steps in evolution of this important characteristic. On the basis of his examination of type material, Ronald Madge invited me to review my concept of the species of the *Phloeoxena picta* group, and this re-examination led to a much improved understanding of these species. Henri Goulet, Richard C. Fox and other members of the Zoology 621 course, to whom I presented a preliminary version of a phylogenetic system for the species of *Phloeoxena*, took the trouble to examine my views in considerable detail. The resulting advice led to development of the pattern of relationships suggested in this paper.

To all of these associates, I am deeply grateful. The magnitude of their contributions reminds me that preparation of a publication is a highly cooperative venture.

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LITERATURE CITED

- Alluaud, C. 1933. Cicindelidae et Carabidae de l'isle Maurice. *Afra*, 7: 1-16.
 Ball, G. E. 1960. Carabidae, Fascicle 4, pp. 55-210. In Arnett, R. H. The beetles of the United States (a manual for identification). Catholic University of America Press, Washington, D. C. xi + 1112 p.
 Ball, G. E. 1970. The species of the Mexican genus *Aztecarpalus*, new genus (Coleoptera: Carabidae: Harpalini). The Coleopterists Bulletin, 24 (4): 97-123.
 Ball, G. E. 1972. Classification of the species of the *Harpalus* subgenus *Glanodes* Casey (Carabidae: Coleoptera). Coleopterists Bulletin, 26 (4): 179-204.
 Ball, G. E. and J. Nègre. 1972. The taxonomy of the Nearctic species of the genus *Calathus* Bonelli (Coleoptera: Carabidae: Agonini). Transactions of the American Entomological

- Society, 98: 412-533.
- Basilewsky, P. 1953. Carabidae (Coleoptera Adephaga). Exploration du Parc National de Upemba. 10. (L'Institut du Parcs Nationales de le Congo Belge) Bruxelles, pp. 1-252.
- Bates, H. W. 1869. On *Coptodera* and the allied genera. Entomologists' Monthly Magazine, 6: 69-80.
- Bates, H. W. 1870. Note sur la synonymie des espèces de coptodérides décrites par M. le Baron Chaudoir et H. W. Bates. Comptes Rendus des Séances de la Société Entomologique Belgique, 1870, pp. xvi-xvii.
- Bates, H. W. 1883. Coleoptera. Carabidae. Vol. 1, part 1, p. 153-256, plates vi - xii. In Godman, F. D. and O. Salvin. Biologia Centrali-Americana.
- Bates, H. W. 1884. IBID, p. 261-299, plate xiii.
- Blackwelder, R. E. 1944. Checklist of the coleopterous insects of Mexico, Central America, the West Indies and South America. Part 1. Bulletin of the United States National Museum, No. 185, pp. 1-188.
- Blanchard, C. E. 1842. In Cuvier, G. Le Regne Animal [Edition Masson, Disciples Edition]. 1836-1849, 557 pages.
- Britton, E. B. 1940. The insect fauna of a nest of the silvery-cheeked hornbill, including the description of *Oecornis nidicola* g. et sp. n. (Col. Carabidae) from Tanganyika. Entomologist's Monthly Magazine, 76: 108-112.
- Britton, E. B. 1941. The Carabidae (Coleoptera) of New Zealand. Part II. Tribes Lebiini and Pentagoncini. Proceedings of the Royal Entomological Society of London, Series B, 10 (10): 185-196.
- Chaudoir, M. de. 1843. Genres nouveaux de la famille des carabiques. Moskoveskoe obschestvo ispytatelei prirody, 16 (III): 383-427.
- Chaudoir, M. de. 1848. Mémoire sur la famille des carabiques. IBID, 21: 3 (I): 3-134.
- Chaudoir, M. de. 1869a. Mémoire sur les Thyréoptérides. Annales de la Société Entomologique de Belgique, 12: 113-162.
- Chaudoir, M. de. 1869b. Memoire sur les coptodérides. IBID, 12: 163-256.
- Csiki, E. 1928. Carabidae, Mormolycinae, Harpalinae I, pars 97, pp. 1-266 (Vol. II). In Junk, W. and S. Schenkling (editors). 1909-1940. Coleopterorum Catalogus. Berlin and s'Gravenhage. 170 parts, 30 volumes.
- Csiki, E. 1932. Carabidae, Harpalinae VII, pp. 1279-1598 (Vol. III). IBID.
- Darlington, P. J., Jr. 1934. New West Indian Carabidae, with a list of the Cuban species. Psyche, 41 (2): 66-131.
- Darlington, P. J., Jr. 1935. West Indian Carabidae II: itinerary of 1934: forests of Haiti; new species; and key to *Colpodes*. Psyche, 42 (4): 167-215.
- Darlington, P. J., Jr. 1937. West Indian Carabidae III: new species and records from Cuba, with a brief discussion of the mountain fauna. Memorias de la Sociedad Cubana de Historia Natural, 11 (2): 115-136.
- Darlington, P. J., Jr. 1939. West Indian Carabidae V. New forms from the Dominican Republic and Puerto Rico. IBID, 13 (2): 79-101.
- Darlington, P. J., Jr. 1957. Zoogeography: the geographical distribution of animals. John Wiley and Sons, Incorporated, New York. 675 pp.
- Darlington, P. J., Jr. 1968. The carabid beetles of New Guinea. Part III. Harpalinae (Continued): Perigonini to Pseudomorphini. Bulletin of the Museum of Comparative Zoology, 137 (1): 1-253.
- Darlington, P. J., Jr. 1971. The carabid beetles of New Guinea. Part IV. General considerations; analysis and history of fauna; taxonomic supplement. IBID, 142 (2): 130-337.
- Dejean, P. F. M. A. 1825. Species general des Coléoptères de M. le Comte Dejean. Paris. Vol. 1,

xxx + 463 pages.

- Dejean, P. F. M. A. 1831. IBID. Vol. 5. viii + 883 pages.
- Duellman, W. E. 1970. The hyliid frogs of Middle America. Volume 2. Monograph of the Museum of Natural History of Kansas, Lawrence, Kansas. p. 429-753, plates 1-72.
- Durham, J. W., A. R. V. Arellano, and J. V. Peck. 1955. Evidence for no Isthmus of Tehuantepec seaway. Bulletin of the Geological Society of America, 66: 977-992.
- Emden, F. I. van. 1942. A Key to the genera of larval Carabidae. Transactions of the Royal Entomological Society of London, 92: 1-99.
- Fabricius, J. C. 1787. Mantissa Insectorum. I. Copenhagen, xx + 348 p.
- Fabricius, J. C. 1792. Entomologia systematica. I, 1. Copenhagen, xx + 330 p.
- Fattig, P. W. 1949. The Carabidae or ground beetles of Georgia. Emory University Museum Bulletin, 7: 1-62.
- Goulet, H. 1974. Classification of the North and Middle American species of the genus *Pelmatellus* Bates (Coleoptera: Carabidae: Harpalini). Quaestiones entomologicae, 10 (2): 80-102.
- Habu, A. 1967. Fauna Japonica. Carabidae, Truncatipennes Group (Insecta: Coleoptera). Tokyo Electrical College Press, HakushinSha Printing Company, Limited, Tokyo, Japan. xiv + 338 pages, 527 figures, Plates I-XXVII, some in color.
- Hansen, W. 1968. Revision des coptoderines d'Afrique. Bulletin et Annales de la Société Royale d'Entomologie de Belgique, 104: 277-363.
- Hennig, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana, Illinois. 263 p.
- Hershkovitz, P. 1972. The recent mammals of the Neotropical Region: a zoogeographic and ecological review, p. 311-431. In Keast, A., F. C. Erk, and B. Glass (editors). 1972. Evolution, mammals and southern continents. State University of New York Press, Albany, New York. 543 p.
- Horn, G. H. 1881. On the genera of Carabidae with special reference to the fauna of Boreal America. Transactions of the American Entomological Society, 9: 91-196, plates 1-10.
- Jeannel, R. 1949. Coléoptères carabiques de la Region Malgache (troisieme partie). Faune de l'Empire francais, XI: 767-1146, Figs. 365-548.
- Jedlička, A. 1963. Monographie der Truncatipennen aus Ostasien-Lebiinae-Odacanthinae-Brachyninae. Entomologische Abhandlungen und Berichte dem Staatliches Museum für Tierkunde in Dresden, 28 (7): 269-579, 244 text-figs., 54 plates, 6 colored.
- Kirby, W. 1825. A description of some insects which appear to exemplify Mr. William S. MacLeay's doctrine of affinity and analogy. Transactions of the Linnean Society of London, 14: 93-110.
- Kirk, V. M. 1969. A list of beetles of South Carolina, Part 1. Northern Coastal Plain. Technical Bulletin 1033: 1-124. South Carolina Agricultural Experiment Station, Clemson University, Clemson, South Carolina.
- Lacordaire, J. R. 1854. Histoire naturelle des insectes. Genera des Coléoptères. Paris. Vol. 1. Cicindelites-Palpicornes, xx + 486 pages.
- LeConte, J. L. 1848. A descriptive catalogue of the geodephagous Coleoptera inhabiting the United States. Annals of the Lycaenum of Natural History of New York, 4: 173-233, 334-474.
- Leng, C. W. 1915. List of the Carabidae of Florida. Bulletin of the American Museum of Natural History, 34 (19): 555-601.
- Leng, C. W. 1920. Catalogue of the coleoptera of America, north of Mexico. Mt. Vernon, New York. 470 pages.
- Lieftinck, M. A. and J. T. Wiebes. 1968. Notes on the genus *Mormolyce* Hagenbach. Bijdragen tot de Dierkunde, 38: 59-68.
- Lindroth, C. H. 1968. The ground beetles (Carabidae excl. Cicindelinae) of Canada and Alaska. Part 5. Opuscula Entomologica, Supplementum 33, pp. 649-944, Figs. 329-480.
- Löding, H. P. 1945. Catalogue of the beetles of Alabama. Geological Survey of Alabama,

- Monograph 11, University, Alabama. 171 pages.
- Maindron, M. 1905. Notes synonymiques sur quelques coléoptères de la famille des Carabidae. Bulletin de la Societe Entomologique de France, 1905, pages 94-95.
- Maindron, M. 1906. Materiaux pour servir a l'histoire des cicindelides et des carabiques. III. Notes sur divers Carabidae de l'Amerique du Sud. Annales de la Societe Entomologique de France, 75: 195-202.
- Maldonado-Koerdell, M. 1964. Geohistory and paleogeography of Middle America, p. 3-32. In Wauchope, R. and R. C. West (editors). 1972. Handbook of Middle American Indians, Volume 1. Natural environment and early cultures, University of Texas Press, Austin, Texas.
- Malfait, B. T. and M. G. Dinkelman. 1972. Circum-Caribbean tectonic and igneous activity, and the evolution of the Caribbean plate. Bulletin of the Geological Society of America, 83: 251-272.
- Martin, P. S. 1958. A biogeography of reptiles and amphibians in the Gomez Farias Region, Tamaulipas, Mexico. Miscellaneous Publications, Museum of Zoology, University of Michigan, No. 101, 102 pages, 7 figures, 4 maps.
- Maslin, T. P. 1952. Morphological criteria of phyletic relationships. Systematic Zoology, 1 (2): 49-70.
- Mateu, J. 1963. Notas sobre tres séries filéticas de Lebiidae (Lichnasthenini Thomson, Singilini Jeannel, Somotrichini nov.) (Coleoptera- Carabidae) y rectificaciones sinonimicas. Annali del Museo Civico di Storia Naturali di Genova, 74: 122-139.
- Noonan, G. R. 1973. The anisodactylines (Insecta: Coleoptera: Carabidae: Harpalini): classification, evolution and zoogeography. Quaestiones entomologicae, 9 (4): 266-480.
- Reichardt, H. 1972. A review of *Eurycoleus* Chaudoir (Coleoptera, Carabidae). Papeis Avulsos de Zoologia, São Paulo, 25 (23): 237-249.
- Reichardt, H. 1974. Monograph of the Neotropical Helluonini, with notes and discussions on Old World forms. Studia Entomologica, 17 (1-4): 211-302.
- Reiche, E. 1842. Coléoptères de Colombie. Revue zoologique par la Societe Cuvierienne, 1842, pp. 238-242, 272-276, 307-314, 374-378.
- Ross, H. H. 1967. The evolution and past dispersal of the Trichoptera. Annual Review of Entomology, 12: 169-206.
- Ross, H. H. 1974. Biological systematics. Addison-Wesley Publishing Co., Inc., Reading, Massachusetts, Menlo Park, California, London, Don Mills, Ontario. Preface, Acknowledgements, Contents, pages 1-345.
- Rousseau, E. 1906. Fascicule 40. Coleoptera. Adephaga. Fam. Carabidae. Subfam. Mormolycinae. 5 p, 1 plate. In Wytsman, P. (editor). 1902. Genera Insectorum, Bruxelles.
- Savage, J. M. 1973. The geographic distribution of frogs: patterns and predictions, p. 351-443. In Vial, J. L. (editor). 1973. Evolutionary biology of the anurans. University of Missouri Press, Columbia, Missouri, 470 p.
- Schaupp, F. G. 1882. Synoptic tables of Coleoptera. Bulletin of the Brooklyn Entomological Society, 5: 64.
- Seidlitz, G. von. 1887-1891. Fauna Baltica. Die Käfer (Coleoptera) der deutschen Ustseeprovinzen Russlands. Königsberg, 192 and 818 p.
- Straneo, S. L. 1969. Sui Carabidi del Chile, raccolti dal Dr. Holdgate della Royal Society Expedition (1958-1959). Annales de la Societe Entomologique de France, 5 (4): 951-974.
- Whitehead, D. R. 1972. Classification, phylogeny and zoogeography of *Schizogenius* Putzeys (Coleoptera: Carabidae: Scaritini). Quaestiones entomologicae, 8 (3): 131-348.